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PARAPATRY IN CLETHRIONOMYS: ETHOLOGICAL ASPECTS OF
MUTUAL EXCLUSION IN C. GAPPERI AND C. RUTILUS

by



EUAN CUTHBERTSON MCPHEE

A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled " Parapatry in Clethrionomys: Ethological aspects of mutual exclusion in C. gapperi and C. rutilus" submitted by Euan Cuthbertson McPhee in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

.....*Wm. A. Fisher*.....
Supervisor

.....*D. J. Ball*.....

.....*Chet Holmes*.....

.....*Fred C. Zwick*.....

.....*William J. L. L. L.*.....
External Examiner

Date *Oct. 21* 1977

ABSTRACT

The Kakisa River, southern Mackenzie District, Northwest Territories, forms part of the common boundary between Clethrionomys gapperi and C. rutilus in northwestern North America. There is no discontinuity in the mosaic of community types at the river, nor are there differences in the known ecological requirements of the two species. Because individuals of each species are occasionally trapped on the side of the river occupied by the other species, the river does not represent a complete barrier, but probably acts as a filter which prevents mass crossing.

Censuses on a pair of 2 ha grids revealed that C. gapperi were consistently more numerous than C. rutilus but seasonal and annual changes in numbers were the same in both species. Mean Inter-capture Distance was somewhat greater for C. gapperi, but the difference was not significant.

Observations of inter- and intraspecific behavior in semi-natural enclosures revealed that both length of time active and distances moved during each 8-hour observation period were greater for C. gapperi than C. rutilus. Yet the rate of occurrence of each species in the range of the other (2-3%) was the same for both. A partial explanation may reside in the observation that C. gapperi was less active in interspecific than in species-true trials, where-

as the activity of C. rutilus increased in interspecific trials.

Four aggressive acts (approach, attack, chase, scent-mark) were subjected to discriminant functions analysis and an index of aggression derived by multiplying the observed frequency of each act by the appropriate discriminant function and summing the resultant figures. Indices of aggression were significantly higher for C. gapperi than for C. rutilus in intraspecific encounters, but the indices did not differ significantly in interspecific encounters. C. rutilus was dominant to C. gapperi in 9 of 13 interactions; no dominance could be determined in the remaining 11 interactions. Aggression did not appear to be important in either inter- or intraspecific encounters; mutual avoidance was the most common response.

Observation of copulatory behavior indicated that male voles were indiscriminate in their mating, although none of the copulations observed produced offspring. Reproductive isolation appears to be reasonably well developed as 77 cross-breeding trials yielded only one hybrid litter; however, species-true breeding trials were less than 50% successful.

While these species are similar morphologically and physiologically species integrity seems to be upheld. In sympatry, these species would be in strong competition, yet neither seems to have a competitive advantage over the other. Thus the parapatric relationship at the Kakisa River appears to be maintained by mutual exclusion.

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INTRODUCTION

(1) The General Problem

Clethrionomys gapperi and C. rutilus are two closely related species of red-backed vole which, while possessing large geographic ranges, have apparently retained a distinct separation at a common boundary. The slight difference in morphological and anatomical features of the two species, and overlap displayed in their serum proteins (Canham and Cameron 1972), suggest a common origin, probably in Eurasia, prior to the Wisconsin or Illinoian glacial period (Holland 1958). The two populations of Clethrionomys must have been separated by more than 2,000 miles during the Wisconsin glacial maxima at 35,000 and 25,000 years B.P., according to the probable extent of continental ice sheets (Hopkins 1967), although it is impossible to say whether they were fully speciated by then. Following the decline from the last glacial maximum, and the re-establishment of an ice-free corridor between Alaska and central North America around 12,000 to 10,000 years ago (Hopkins ibid), the two species extended their geographic ranges (Macpherson 1965) until they came into contact along a line from Great Slave Lake to the Pacific Ocean (Banfield 1974).

In both Eurasia (Ognev 1950) and northwestern North America (Bee and Hall 1956, Manning 1956), C. rutilus has been recorded throughout tundra and boreal forest. Martell (1975) suggested that tundra constitutes suboptimal habitat, so that C. rutilus can be regarded as primarily a forest species which has secondarily exploited tundra habitats. C. gapperi on the other hand, is a more strictly boreal forest species. It is not found far beyond the tree-line in the Ungava Peninsula, in spite of the absence of any definite barrier (Banfield 1956), while near Churchill, Manitoba, it is only found in the tundra in periods of high numbers (Smith and Foster 1957). Thus it seems that C. rutilus has not expanded to the theoretical southern extent of its range when C. gapperi is present, and C. gapperi has not reached its potential northern limit in the presence of C. rutilus. Instead, a conterminous boundary has been established between the species from Hudson Bay to the Pacific Ocean (except where separated by Great Slave Lake), and a situation of parapatry now appears to exist.

Instances of parapatry between species are relatively rare, since they generally represent but a brief period between allopatry and sympatry. In his description of the process of speciation in more than 70 species of New Guinea montane birds, Diamond (1973) characterized eight stages, of which the parapatric condition is but one.

In the tropical situation, with its multiplicity of species representing many different stages in the speciation process, parapatry is more easily envisaged than in the boreal forest where there are few species of cricetid rodents with which to make comparisons. Dobzhansky and Spassky (1959) observed the process of species formation in the superspecies Drosophila paulistorum, although it is acknowledged that such events are relatively rare, since the critical stages of the speciation process are probably passed rather rapidly. Cognizant of this problem, then, I will now consider the particular situation of parapatry in Clethrionomys at the Kakisa River.

(2) The Situation at the Kakisa River

Little is known of the exact demarcation of the range of each species; traditionally, there has been no overlap acknowledged (Hall and Kelson 1959). Common boundaries have been known to exist for at least 30 years in northern British Columbia (Rand 1944) and 16 years at the Kakisa River (Fuller 1969). In the former area, Canham and Cameron (1972) suggested that marginal montane habitat has kept the species apart. Although Fuller (ibid) cited four instances of C. rutilus occurring on the "wrong" side of the Kakisa river, there is no evidence of hybridization at this boundary. Discovery of animals displaying intergradation of morphological features in the vicinity of Churchill, Manitoba, however, suggests hybridization there (Smith and

Foster 1957).

The Kakisa River, with an average width of about 100 m does not represent a sufficient barrier to movement of voles, since at some time in the past C. rutilus crossed the more expansive Mackenzie River and now occurs on most of the islands near Fort Providence, Northwest Territories. Crossings of open bodies of water, from 8 to 233 m wide, has been achieved by Peromyscus leucopus (Sheppe 1965) and inter-island migrations have also been demonstrated by Microtus pennsylvanicus in Newfoundland, over distances ranging from 60 to 750 m (Pruitt and Riewe, reported in Crowell 1973). The Kakisa River is frozen over for at least 4 months of the year, which would facilitate traversing the river in winter. Crowell (ibid) noted, however, that C. gapperi and P. maniculatus tended to exhibit considerably lower dispersive abilities than M. pennsylvanicus, and that C. gapperi required larger founder populations than P. maniculatus to become established on islands.

The presence of a bridge carrying the Mackenzie Highway across the Kakisa River for the last 16 years could also affect movement of either species into the range of the other. Buckner (1957) has shown that roadways up to 20 m wide did not hinder movement of C. gapperi. During the winter of 1974-5, P. maniculatus crossed the Mackenzie Highway in the vicinity of Heart Lake several times during the same night (pers. obs.). That same winter, a live

masked shrew (Sorex cinereus) was apprehended by a dog halfway across the frozen surface of the Hay River, Northwest Territories, a river which is at least twice as wide as the Kakisa (Rick Geddes, pers. comm.). However, Oxley et al. (1974) found that C. gapperi did not cross any of the roads they studied, which varied in width from 11 to 137 m, and they suggested that highways with clearances of 90 m or more were as effective barriers to the dispersal of small forest mammals as bodies of fresh water twice as wide. Cameron (1962) also demonstrated that an artificial land-bridge 25 m wide and 1.6 km long was insufficient to induce emigration of mammals from mainland Nova Scotia to Cape Breton Island. In spite of the limitations on movement imposed by physical obstructions, dispersing voles are capable of covering considerable distances through unfamiliar terrain (Watts 1970a, Hilborn and Krebs 1976). Thus it seems likely that the Kakisa River acts as a filter rather than a barrier to movement of Clethrionomys.

Most studies of sympatric species have indicated that separation is maintained by some form of resource allocation (Vaughan 1974), although mechanisms involved differ among different species. Interspecific aggression is held responsible by various authors for maintenance of separation between many species of small mammals, such as Sigmodon fulviventer and S. hispidus (Petersen 1973), five species of Microtus (Colvin 1973), M. pennsylvanicus and

Dicrostonyx groenlandicus (Banks and Fox 1968), Peromyscus species and Mus musculus (King 1957, Caldwell and Gentry 1965, Sheppe 1967), Thomomys bottae and T. talpoides (Baker 1974), and four species of Eutamias (Heller 1971).

Closer examination of competitive situations has shown that so-called sympatric species tend to exhibit habitat segregation and mutual avoidance rather than direct conflict, as for example Eutamias dorsalis and E. umbrinus (Brown 1971), M. pennsylvanicus and M. montanus (Murie 1971) and M. pennsylvanicus and C. gapperi (Morris 1969, Grant 1970a, Morris and Grant 1972, Grant 1972). The relative importance of these two forces in shaping the distribution of species is not always easily assessed, as interspecific aggression often leads to habitat segregation and, conversely, habitat segregation tends to reduce competitive interactions (Koplin and Hoffman 1968). The absence of one species from a particular habitat in which it normally occurs, however, often permits spread of another species into that area, as suggested with M. pennsylvanicus and C. gapperi (Clough 1964, Morris 1969). A similar process of mutual avoidance could well be the basis for a separation of the two species of Clethrionomys at the Kakisa River. With more distantly related species occupying the same habitat, segregation has often been achieved on the basis of different food requirements or different times of activity, or both (Vaughan 1974, Andrzej-

jewski and Olszewski 1963).

Several studies have already been conducted on certain ecological aspects of C. gapperi and C. rutilus in the southern Mackenzie area, which indicate their close phylogenetic relations. Population fluctuations and reproductive strategies of the two species have been shown to be essentially the same, and no obvious habitat differences which might explain separation can be ascribed to either side of the Kakisa River (Fuller 1969). Frequently, the boundary between two species coincides with a sharp habitat change, so that the competitive advantage of either species in its habitat is lost when in the habitat of the other. Thus, a narrow zone of overlap with a certain amount of interspecific aggression may become established, as in Eutamias dorsalis and E. umbrinus (Brown 1971). Clethrionomys species differ markedly from P. maniculatus in dietary preferences, but no difference has been shown between C. gapperi and C. rutilus (Dyke 1971). While there is a broad spectrum of serum proteins common to both species (Canham and Cameron 1972), considerable differences in levels of activity have been observed (Murie and Dickinson 1973, Stebbins 1972, Friesen 1972). Thus it would seem that if an isolating mechanism is at work, it may be achieved by some form of behavioral difference. If the species have only reached the common boundary in relatively recent times, however, behavioral

differences would not be well developed and one would expect them to be slight and subtle.

Another aspect of closely related species occurring in sympatry is the low level of cross-breeding. In classical terms, a species was defined on the basis of the ability to interbreed and produce viable offspring, which in turn were capable of breeding (Mayr 1963). Such a cut-and-dried definition of species has been found inadequate (Dobzhansky 1972), since cross-breeding has been achieved in the laboratory with species of Drosophila (Sturtevant and Dobzhansky 1936, Miller 1939 and 1941, Patterson 1954) and some of these hybrid crosses have proved fertile (Miller 1941, Patterson ibid.). More recently, hybridization between species of Drosophila has been observed in the wild (Carson et al. 1975). In a population comprising two closely related species in an area of sympatry, 2% of the naturally occurring individuals were hybrids yet, despite hybridization, the essential integrity of each separate gene pool appears to be maintained.

Cross-breeding has also been induced in several species of small mammals in the laboratory, including species of Peromyscus (Dice 1937, Clark 1966, Bradshaw 1968), Microtus (Hatfield 1935, Pokrovskii et al. 1970), and Clethrionomys (Spannhof 1960, Rauschert 1963, Zimmermann 1965, Grant 1974). Prior to this study, only one instance has been reported of cross-breeding in Clethrion-

omys gapperi and C. rutilus in captivity (Fuller, pers. comm.). However, cross-breeding under laboratory conditions does not constitute proof for cross-breeding in the field. Even when cross-breeding is achieved, reduction in reproductive success often occurs, usually in terms of litter size, hybrid viability or relative fertility of hybrids, factors which would all favor selection against hybridization in nature. Reduced reproductive success has even been shown in certain subspecies of small mammals, notably in island subspecies of C. glareolus (Godfrey 1958), and total reproductive isolation has been observed in subspecies of Mus musculus (Hunt and Selander 1973). Thus, if reproductive success is so affected at the subspecific level, one would expect that it is affected even more between most species.

Furthermore, in apparent contradiction to the Gausean Principle, closely related species of Drosophila have been shown to coexist, albeit at lower population densities than each species on its own (Ayala 1972). Richmond and Dobzhansky (1976) have also shown that ethological isolation among the semispecies of D. paulistorum is strong enough that two or three semispecies are able to coexist sympatrically in many localities. Thus much of the isolation between closely related species is generally achieved by prezygotic ethological processes and, should this fail, by reduced reproductive success, i.e. postzygotic processes.

Since the production of less fit cross-bred individuals is wasteful both genetically and energetically, it would seem that evolution of differences in behavior would tend to be favored in areas where similar species have recently come into contact.

It is a truism that, apart from "chance" introductions e.g. floating across on a log, only dispersing voles would cross the Kakisa River. Howard (1960) suggested that there is a strong innate predisposition for some individuals to disperse, and it has also been suggested that dispersal has a genetic basis (Chitty 1967, Myers and Krebs 1971, Krebs et al. 1973 and 1976, Hilborn 1975), although conclusive evidence of such a connection has yet to be shown. Christian (1970) proposed that there is a direct link between aggressive behavior and dispersal, especially in Microtus species, and while some work supports this notion (Healey 1967), other workers have presented data to the contrary (Krebs et al. 1973, Rose and Gaines 1976). Thus it is not easy to predict the relative success of individuals of each species in colonizing the opposite bank based on differing levels of aggression, which has been shown between the two species (Murie and Dickinson 1973).

The role of dispersal in regulating population density (Lidicker 1962 and 1973) and in occupation of depopulated areas (Van Vleck 1968) is generally accepted, al-

though how such roles would affect the dispersal of individuals from a peak population into an area already occupied by a closely related species in the same phase of population is difficult to envisage. Furthermore, migrant Clethrionomys have been found to be qualitatively poorer than settled individuals (Kozakiewicz 1976), which suggests that migrants may be less fit to deal with the competitive situation awaiting them on the other side of the river. Thus while dispersal doubtless plays an important role in the Kakisa River situation, the nature of the dispersers would affect the ability to colonize the range of the other species.

Having acknowledged the relatively poor dispersive abilities of Clethrionomys (Grant 1970b, Crowell 1973), it is still possible that small breeding colonies of either or both species have already become established on the opposite side of the river. Thus the question is raised as to whether the rate of flow of individuals across the river could be sufficient to establish and sustain a beach-head, as has been suggested for Microtus and Clethrionomys in aspen parkland (Morris 1969), or whether the rate of extinction is too great for such colonization to occur.

From the foregoing considerations, then, and in acknowledgement of the fact that very little work has been conducted on these two species at the boundary formed by

the Kakisa River, I embarked upon the present study. The hypotheses I set out to investigate were:

Main Hypothesis

That the Kakisa River acts as a filter to the movement of the two species of Clethrionomys; and that behavioral interactions are involved in the maintenance of spatial segregation of these species.

Sub-hypotheses

(1) That individuals of each species can and do cross the Kakisa River to invade the range of the other species, and that the majority of such crossings are accomplished during the winter.

(2) That reproductive isolation is sufficiently well developed to prevent hybridization of the two species in this area of potential sympatry.

(3) That if the levels of activity differ markedly in the two species, the migration of the more active species across the river would tend to occur more frequently than that of the less active species.

(4) That specific behavior patterns of each species are modified by the presence of the other species, so that aggressive interactions between the two species are reduced and mutual exclusion is achieved.

METHODS

The main study was carried out at the Kakisa River, Northwest Territories ($60^{\circ} 59'N$, $117^{\circ} 16'W$), where a common boundary between Clethrionomys gapperi and C. rutilus is found (Figs. 1 and 2). There were several different aspects to the research, as follows:

(1) Live-Trap Plots

Two square grids of 1.8 ha each were established either side of the Kakisa River (Fig. 3) in heterogeneous habitat, comprising black spruce (*Picea Mariana*), white spruce (*Picea glauca*), tamarack (*Larix laricina*) and muskeg. Trap locations were marked out by means of numbered stakes, 15 m apart in the form of a ten-by-ten grid, and traps were located within 2 m of the stakes. This permitted traps to be located in areas where vole activity would be most likely, e.g. next to or underneath fallen logs, in runways in the moss, etc., rather than in exposed areas where voles would rarely be found. The types of traps used were mainly Longworth's and some Sherman 22 x 10 x 8 cm traps for the first two summers, but by the third summer, only Longworth's were used.

The trapping schedule was as follows: traps were provided with sunflower seeds, a chunk of standard laboratory mouse chow and terylene nesting material, and were

Figure 1. Map of North America showing distribution
of Clethrionomys gapperi and C. rutilus.

Inset is shown in more detail in Figure 2.

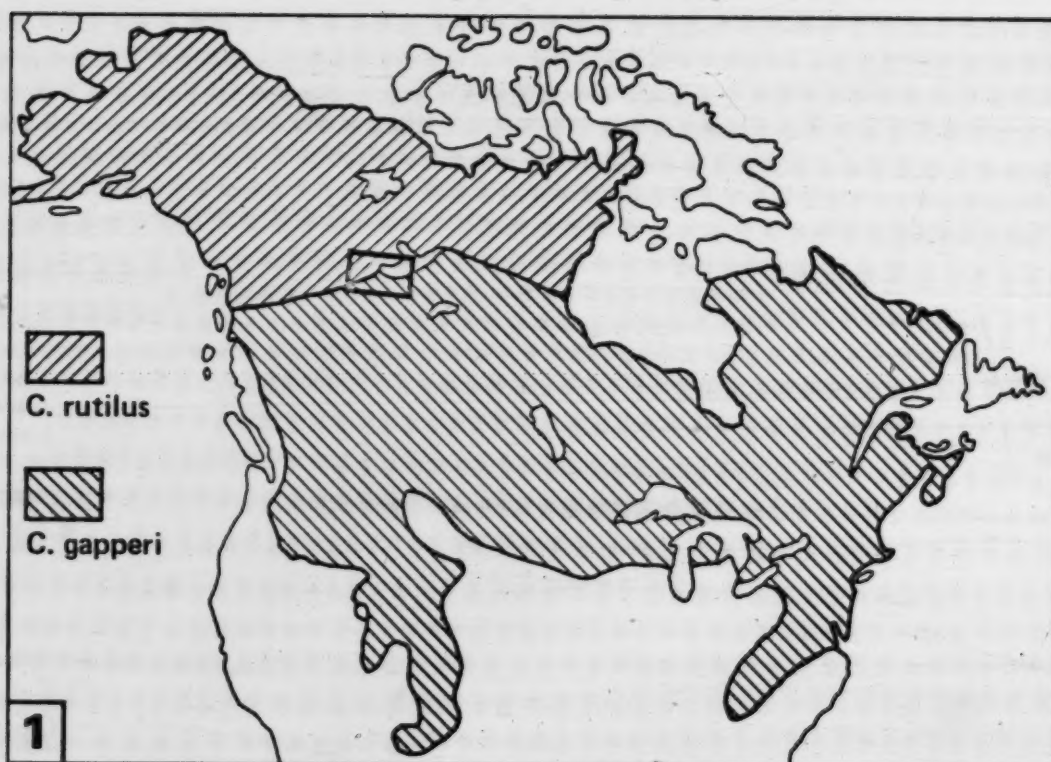


Figure 2. Map of inset from Fig. 1 showing the boundary of the two species at the Kakisa River, N.W.T. and the location of main study site.

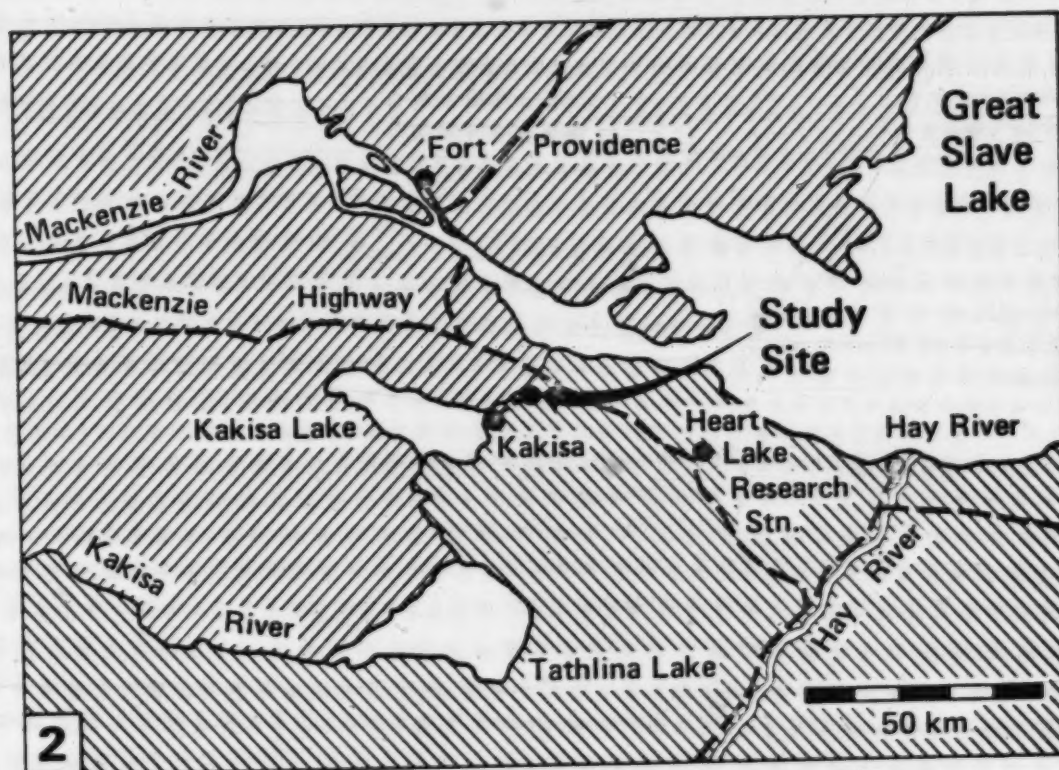
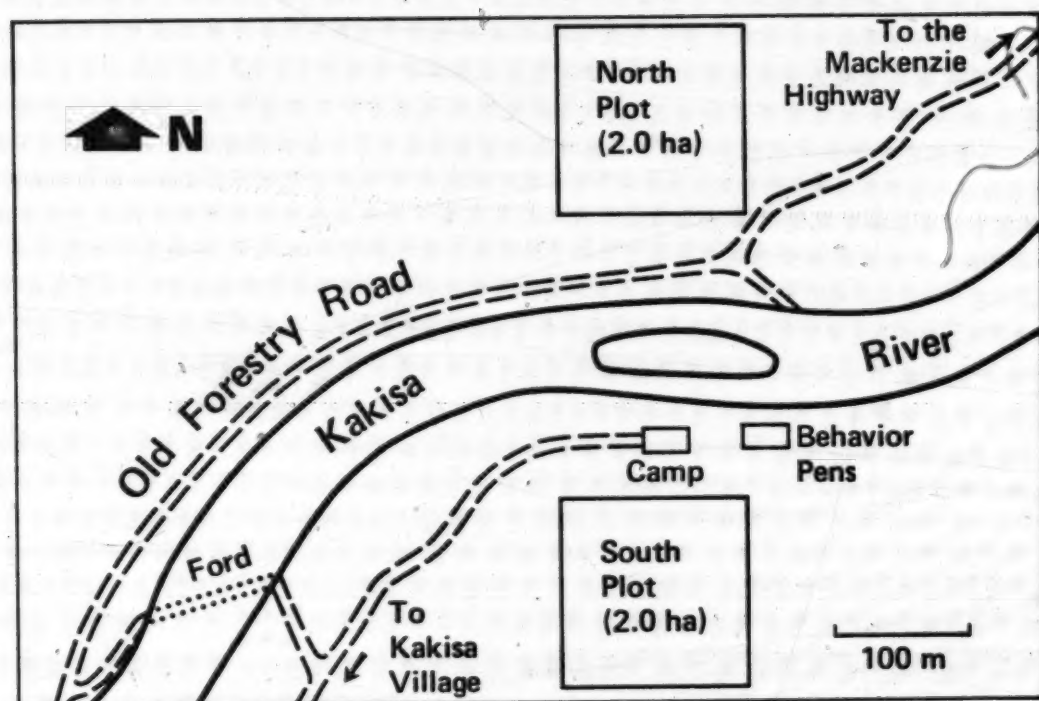


Figure 3. Map showing the location of live-trap plots
and behavior pens at the Kakisa River.



laid out at each location during late afternoon of the day preceding the first trap round. No pre-baiting was carried out. Trap-rounds were made at 0600 hr and 1800 hr every day for 4 days, traps being closed during the 1800 hr round of the fourth day and gathered in on the following day. During the summer of 1973, six such sessions were carried out between mid-May and early September; in 1974 and 1975, three sessions were carried out and in 1976 only one trap session in mid-June was implemented.

Each animal captured was marked by toe-clipping and weighed to the nearest 0.5 g by means of a spring balance; lengths of body (snout-vent), tail and right hind foot were measured; the reproductive status of the individual was assessed by external examination and the trap location was noted.

(2) Behavior Experiments

Observations were made on behavior of Clethrionomys gapperi and C. rutilus in the field, at their common boundary. Fuller (1969) provided a detailed description of the location and habitat of this area. The behavior experiments were conducted in large seminatural pens, providing conditions somewhat between those of small open-field arenas commonly employed by workers interested in aggressive encounters among small mammals (Clarke 1956, Johst 1967, Murie 1971, Turner and Iverson 1973) and field enclosures used to study dynamics of small mammal popu-

lations in a portion of their natural habitat (Caldwell and Gentry 1965, Koplín and Hoffmann 1968, Krebs, Keller and Tamarin 1969, Grant 1969 and 1971, Morris and Grant 1972, Herman 1975). My pens, with their floor covering of moss and fallen logs, provided a far more diversified terrain than arenas and, being considerably larger, enabled stressful situations to be reduced or even avoided by the interacting voles. Observations were also carried out over a much longer period of time than that employed in arena studies, so that a more normal level of activity and repertoire of behavior patterns could be observed.

(a) The Pens

Experimental pens were constructed in an area of mature jack-pine next to the Kakisa River (Figs. 2 and 3, Plates 1 and 2) and consisted of two pairs of 2.4 m by 2.4 m enclosures connected by a 4.8 m runway (Fig. 4). Walls 0.6 m high were made from sections of sheet galvanised steel screwed together and cemented at the base. Pen floors were scraped clear of moss and wire mesh was laid down, to prevent voles from digging their way out, then the moss was replaced. Several fallen logs were added, to recreate the forest floor conditions as far as possible, and then a wooden nest box, feeding hopper and water bottle were added to each pen (Plates 3 and 4). The runway floors were made of plywood. A wooden observation tower, 1.5 m by 1.5 m by 1.0 m, located midway between the pens and to

Figure 4. Layout of the behavior pens.



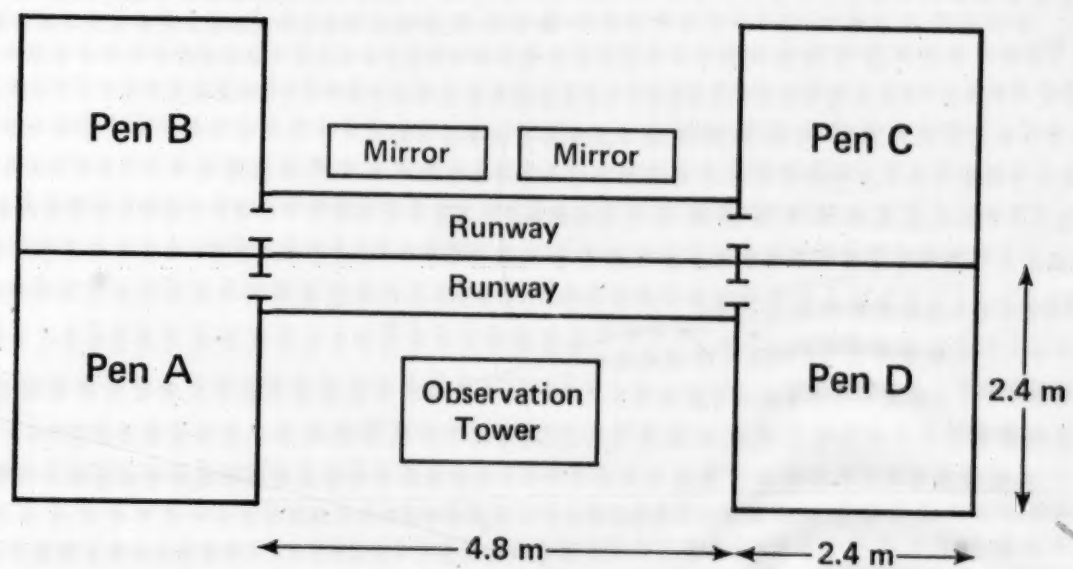




Plate 1. General view of the experimental pens and observation tower.

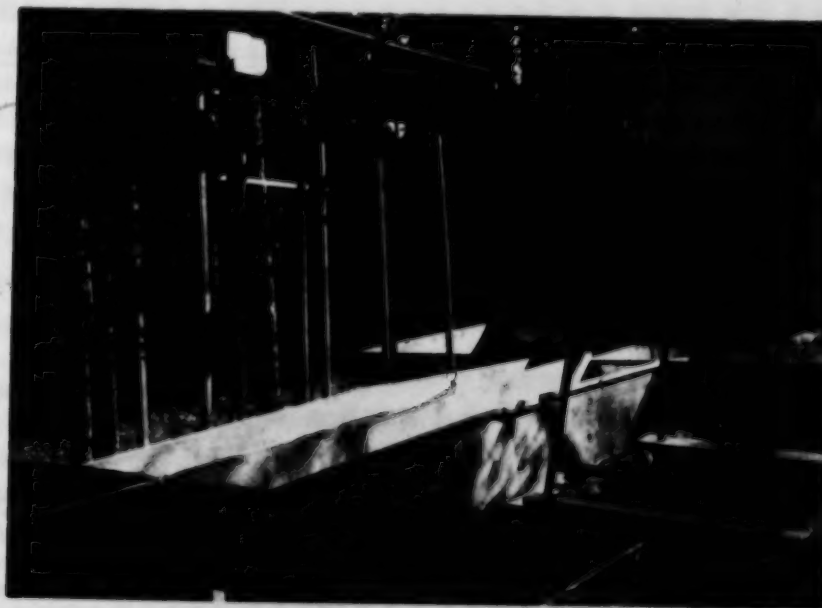


Plate 2. View of the observation tower and runways to show positioning of mirrors.

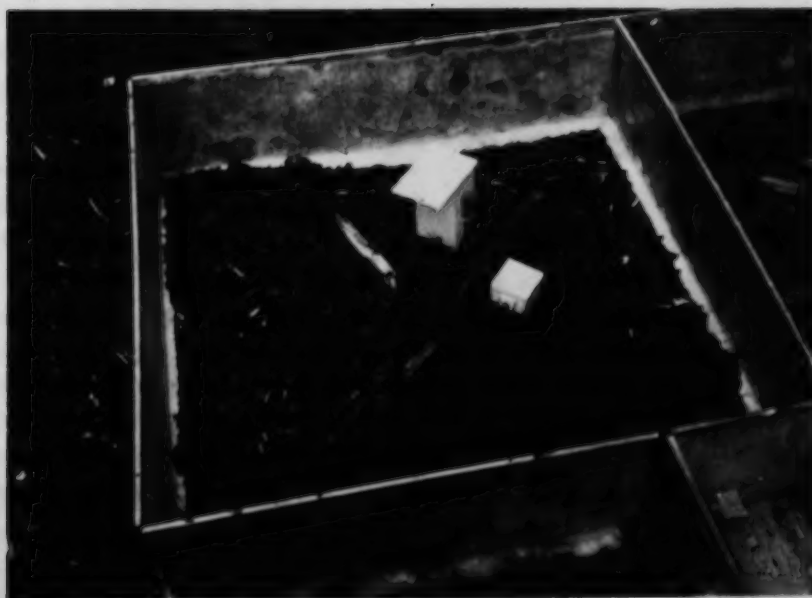


Plate 3. View of pen A from the observation tower. Note the inclusion of logs, nest-box, feeder and water-bottle.

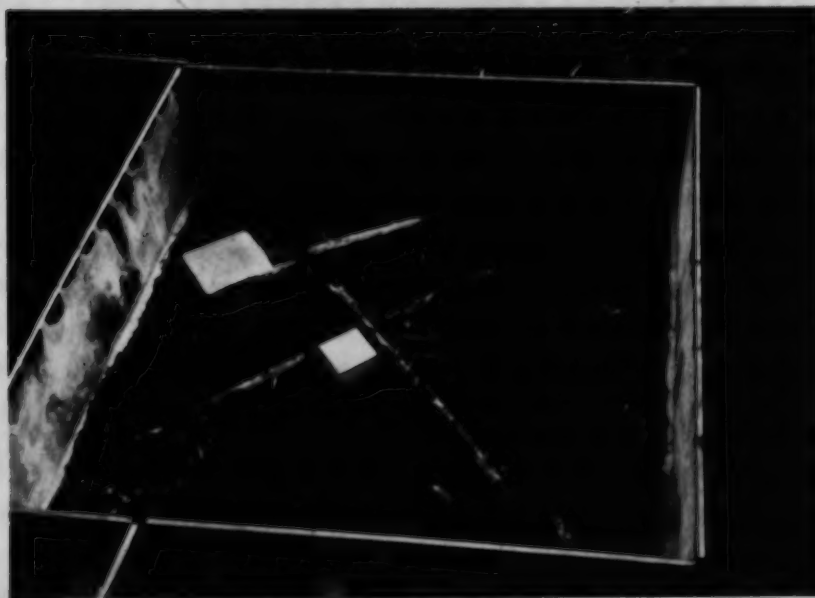


Plate 4. View of pen D from the observation tower. Note the wire-mesh floor bared of moss by vole activity (also pen A, above).

one side of the runways and standing 1.3 m above ground level, provided shelter for the observer and minimised disturbance of the voles by the observer. Large windows on three sides of the observation tower provided good visibility of at least 80 percent of each pen area, the nearside walls preventing a complete view of the pen area (Plates 3 and 4). Two mirrors, 1.8 m by 0.4 m each, were positioned at 45° in front of the observation tower and 2.5 m above the runways, so that movement of voles between the pens could be seen.

(b) The Experimental Animals

Voles were captured from May through August, 1973 to 1974, using Longworth traps baited in the same manner as for the live-trap plots. Most trapping was carried out within 0.5 km of the river and in most cases at least 1.0 km away from the live-trap plots, so that no marked animals would turn up among wild-caught individuals. A decline in populations in 1975 necessitated trapping of voles from further afield for use in the behavior observations, from Fort Providence to the northwest (60 km) and Heart Lake Biological Station to the southeast (40 km). Some animals were also trapped in the camp, but no marked individuals were ever taken. Only voles caught near the boundary were used in interspecific trials, whereas voles from either source were used in intraspecific trials.

Wild-caught voles were brought to the Kakisa camp,

weighed, measured and toe-clipped, and their reproductive status was assessed by external examination. In most cases, only sexually mature animals that weighed at least 20 g were used in behavior trials, although shortage of animals during the summer of 1975 meant that a few underweight individuals were used. Male voles were housed individually in shoebox cages (28 x 18 x 13 cm), females in rat-size cages (45 x 20 x 13 cm), and both were offered standard laboratory mouse chow and water ad libitum. The cages were maintained in an outdoor shelter under the normal regime of temperature and daylight. Most animals were caged for 1 to 4 weeks prior to use in the pens.

(c) Observations

During the summer of 1973 several preliminary trials were conducted to see how "mouse-proof" the pens were, and to formulate a system of recording the observed behavior. To determine optimum time for observing vole activity, a 4-day set of observations was carried out, using Clethrionomys gapperi in the left-hand pens and C. rutilus in the right-hand pens, male versus male and female versus female. In this trial, the runway doors were kept closed, and behavior was recorded by means of a shorthand notation of activity.

On the basis of preliminary trials, and findings of other workers (Stebbins 1972, Friesen 1972), it is clear that both species of Clethrionomys exhibit peaks of

activity around dawn and dusk. Thus to obtain maximum activity while limiting observations to periods with sufficient daylight, each trial was conducted over two 4-hour periods, from 1700 to 2100 hr in the evening and from 0600 to 1000 hr the following morning. Observations were made using groups of three animals per trial, six trials of each of the four possible combinations of voles being carried out for males (3 C. gapperi; 2 C. gapperi + 1 C. rutilus; 1 C. gapperi + 2 C. rutilus; 3 C. rutilus). For females, only two of the possible combinations were used, either 3 C. gapperi or 3 C. rutilus. The decision to use combinations of three animals per trial instead of two was made when it was noted that pairs of animals rarely ever interacted.

A number of trials conducted during the summer of 1974 used voles from earlier trials, animals being placed in triplets according to their previous experience, i.e. three animals with two previous trials, three animals with three previous trials, etc. These trials were soon discontinued since the effect of previous experience (Russell and Williams 1973) in the pens on behavior of voles was noticeable in subsequent encounters. Accordingly, data are only used from animals which had no previous pen experience, such that details of initial reactions of individuals to each other, establishment of hierarchies and differences between species in these respects could be

ascertained.

Triplets of voles used in each trial were composed of similar weight animals as much as possible, to reduce effect of body weight on dominance of individuals (Grant 1970a). About an hour before commencement of each trial, voles were weighed and marked for identification by clipping fur on the back of each. The animals were introduced to the runway at the centre, one at a time, and each one allowed to enter either pen before the next one was introduced. Once all three voles were in the pens, observations from the tower were commenced, recorded by means of a cassette tape recorder and transcribed at a later date. Details of location, minutes active, type of activity and description of the interactions were recorded for each animal. By using the record of locations of individual voles in conjunction with a scale map of the pens, it was possible to calculate distance covered by each animal accurately. At the end of each behavior trial, voles were removed from the pens and returned to their cages. Between trials, nest boxes were washed out and new terylene nesting material was added, to reduce the known effect of the odor of other animals on behavior (Whittier and McReynolds 1965, Archer 1968, Jones and Nowell 1973a).

Two sets of breeding behavior trials were also conducted during the summer of 1974, to determine if there

was evidence for reproductive incompatibility. In each trial, pen doors were closed, two fecund females of each species were introduced into the pens and the process of settling down was observed from the time of introduction at 1700 to 2100 hr and again the following morning from 0600 to 1000 hr. Just prior to introduction, nesting material from the cage of each female was placed in the nest box of each female's pen. Twenty-four hours later, a male vole was introduced into each pen, such that there was a cross-specific and a species-true pair of each possible configuration. Subsequent behavior was recorded from 1700 to 2100 hr and from 0600 to 1000 hr the next day. Voles were then removed from the pens and returned to their own cages, and females were checked regularly to see if observed copulations resulted in pregnancies.

A thermohygrograph was in operation continuously during the three summers, a maximum-minimum thermometer was read daily and a general note of the prevailing weather conditions before, during and after each observation period was made (cloud description, wind strength and direction).

(3) Breeding Experiments

The first cross-breeding experiments were conducted from January until April, 1974, at the Department of Zoology of the University of Alberta in Edmonton. A small number of C. gapperi from Heart Lake Biological Station, Northwest Territories, and Ministik Lake, Alberta (50 km southeast of

Edmonton) and some C. rutilus from near the Kakisa River, Northwest Territories, and Inuvik, Northwest Territories, were used in trials of species-true and cross-specific breeding. The voles were trapped at the end of summer of 1973 and were brought to the University and installed in a controlled environment room under a regime of 8 hr daylight, a temperature of 5°C and relative humidity of 40% for six weeks. Over the next six weeks, light was increased by one hour per week, temperature by 2-3°C per week, and humidity was held constant. After this 12 week period, light, temperature and humidity regimes were left unchanged and pairing of animals for breeding was commenced. Throughout the period, voles were housed individually in rat-size cages (except during breeding trials when males were introduced into the cages of the females) and were provided water and mouse-chow ad libitum, the females receiving a high-protein chow and green barley shoots at intervals to help bring on reproductive condition. Males were left with females for 2 weeks and on removal, females were left for a further 2 weeks before being checked for pregnancy. Non-pregnant females were used again in breeding pairs, while pregnant females were left to raise their litters.

Another set of cross-breeding experiments was conducted during the winter of 1974/5 at Heart Lake Biological Station using litters of wild-caught voles which had been born

and raised in captivity. In this instance, however, it was not possible to control environmental conditions as closely as the previous experiments in Edmonton. From mid November to early January, the weekly light regime was increased from 12 hr per day to 18 hr per day and the temperature was maintained around 15-20°C. No control of the humidity regime was possible. All voles were housed individually in shoe-box cages and provided mouse-chow and water ad libitum, females being given high-protein chow. Species-true and cross-specific breeding trials were attempted on the same basis as previously from late August 1974 until mid February 1975. Then the stock of voles, already somewhat depleted from natural or stress-induced mortality (from confinement together during the breeding trials) was killed and either autopsied or fed to captive pine marten (Martes americana) which were part of another research project being conducted at Heart Lake at the same time.

The main set of cross-breeding experiments was carried out during the summers of 1974 and 1975, however, with voles that had already been used in behavior experiments in the pens. Females, housed in rat-sized cages and fed a preferential diet of high-protein chow, had a male vole introduced to the cage for 2 weeks. Two weeks after the male was removed, they were examined to determine if any were pregnant. Pregnant animals were permitted to

raise their young while non-pregnant voles were often paired again to see if further attempts would induce breeding. Most voles were autopsied at the end of summer to assess reproductive condition of the animals.

(4) Radio Telemetry Study

Activity of a small number of voles of each species was monitored in a 0.09 ha enclosure in undisturbed jack pine forest during the winter of 1974/5 at Heart Lake Biological Station. Details of the telemetry system are in Chute et al. (1974). The original intention of the study was to introduce one of each species into the enclosure and to track the two voles simultaneously over a period of 3-4 days (the usual life-span of the transmitter battery) by means of the semi-automated receiver system which was designed to scan the antenna wires and to print out resulting locations of the animals at certain set intervals of time. From this information it was hoped that details of interactions of the two species under an undisturbed cover of snow could be ascertained and related to the situation at the Kakisa River. Although a number of attempts were made at tracking pairs of voles, a series of malfunctions of the semi-automated system only permitted tracking of single voles.

Experimental animals were trapped either side of the Kakisa River during August and September 1974, housed individually in rat-size cages at Heart Lake, provided water

and standard mouse chow ad libitum, and maintained in temperature and light conditions approximating those of the natural environment. In November, cages were moved into a blacked-out room kept at about -5°C , in an attempt to simulate conditions experienced within the subnivean space. Water bottles were replaced by snow during this period.

7 Most animals used for radio tracking were adults, or at least sub-adult, as they were all at least 19.0 g weight. At least 3 days before release into the pen, each vole was anaesthetized with ether and fitted with an inactive transmitter. Prior to release the transmitter was activated by soldering the battery connection, the animal was weighed and then released at the edge of the enclosure by means of one of 10 wooden chimneys located around the perimeter, which permitted direct access to the subnivean space without disturbance to the snow layer. Monitoring of activity began immediately and was carried out for as long as the transmitter gave a reliably strong signal, usually 3-4 days. The sampling time interval was set at 5 minutes, to coincide with the 5 minute sampling period employed in the behavior experiments at the Kakisa River. Thus in each 24 hr period a total of 288 fixes on the position of each animal was obtained.

During the radio tracking experiments, air and subnivean temperatures were recorded four times daily and barometric pressure was noted once a day. Periodic snow

surveys were made in the vicinity of the enclosure, when snow was sampled for depth, density, hardness and crystal size of each layer.

After each experimental run, animals were recaptured in live-traps placed inside the chimneys, radio transmitters were removed and voles were returned to their cages. A number of voles proved notoriously difficult to recapture and thus remained in the pen during subsequent trials. Others died during the experimental run and so were not retrievable from the enclosure. One or two animals also managed to slip out of their radio collars and, like the untrappable voles, were possibly active during subsequent trials.

(5) Confirmation of Species

As I worked at the common boundary of these species of Clethrionomys, it was of importance to be able to confirm that each individual used in the behavior and activity experiments was indeed the species it was deemed to be on the basis of external features. For most individuals, this was done by means of (a) electrophoresis of the plasma proteins and subsequent classification by means of the transferrins and albumins present and (b) measurement of the anterior palatine foramen and noting whether the post-palatal bridge was fused or incomplete.

(a) Electrophoresis of the Plasma Proteins

Following the behavior and breeding trials, voles

were taken to Heart Lake where they were bled from the suborbital sinus by means of a sterilized Pasteur pipette and autopsied. Cells and serum were separated by centrifuging the blood at 5000 G for 2 minutes and the serum was stored in a chest freezer at -10°C . The sera were transferred to Edmonton in a Dewar flask chilled with carbon dioxide "snow" generated from an inverted cylinder of liquid CO_2 , and stored at -10°C once more until electrophoresis was carried out, usually within three months. Some sera were not run until 12 months after collection but, on the basis of runs on the same sera at 3 and 12 months, there appeared to be no significant deterioration in the transferrin and albumin bands on which species confirmation was based.

Disc gel electrophoresis was used to separate the serum proteins (Davis 1964). One or two minor alterations to Davis's technique were made in this study; the order of making up gels was reversed. The sera were diluted 1:1 with 10% sucrose solution and 0.015 ml of serum mixture was layered on top of each gel column. A current of 60 milliamps was used during the electrophoretic run, which generally took about 1 hour. Coomassie Blue was employed as a general protein stain and produced clear definite dark blue bands within the gel. The location of albumins and transferrins was achieved by noting the size and distribution of the various bands relative to each

other; the relative densities of the bands were also noted when the gels were run through a spectrometer and a graphical trace of the transmission of light through the bands was obtained.

(b) Measurement of Skull Characteristics

Skulls were retained from most of the voles used in behavior and breeding trials. Segregation according to species was achieved on the basis of the length/width ratio of the anterior palatine foramen and the condition of the post-palatal bridge (Hall and Kelson 1959) for nearly all specimens.

RESULTS

(1) Demography of the Two Clethrionomys Populations

Populations on both sides of the Kakisa River followed the same general trend (Fig. 5); the low number of animals at the beginning of summer, consisting of overwintered individuals, is supplemented by first litters of the year by mid-summer and (in 1973 and 1974) reached a peak towards the end of the summer, by which time most of the overwintered voles had died off, and the early summer cohort was joined by the mid and late summer cohorts. There is a considerable difference in density of Clethrionomys on the two plots from year to year (peak densities for 1974 are: C. gapperi 30 voles/ha and C. rutilus, 9 voles/ha) but the densities were strongly correlated (Fig. 6, $r=0.957$, $df=11$, $p<0.001$). I cannot say whether this reflects a real difference in the densities of the two species all along the Kakisa River, since the plots are relatively small, although Newson (1963) observed differences in numbers and other population parameters in two neighbouring populations of C. glareolus. It could be that the north plot includes a greater area of unsuitable habitat than the south plot. The latter possibility is supported by evidence of differing soil types, and hence vegetational associations,

Figure 5. Total numbers of voles trapped on each live-trap plot per trap session, 1973-1976.

(The six trap sessions in 1973 were late May, mid-June, early July, late July, early August and late August. The three trap sessions in 1974 and 1975 were late May, mid July and late August. The one trap session in 1976 was in early June).

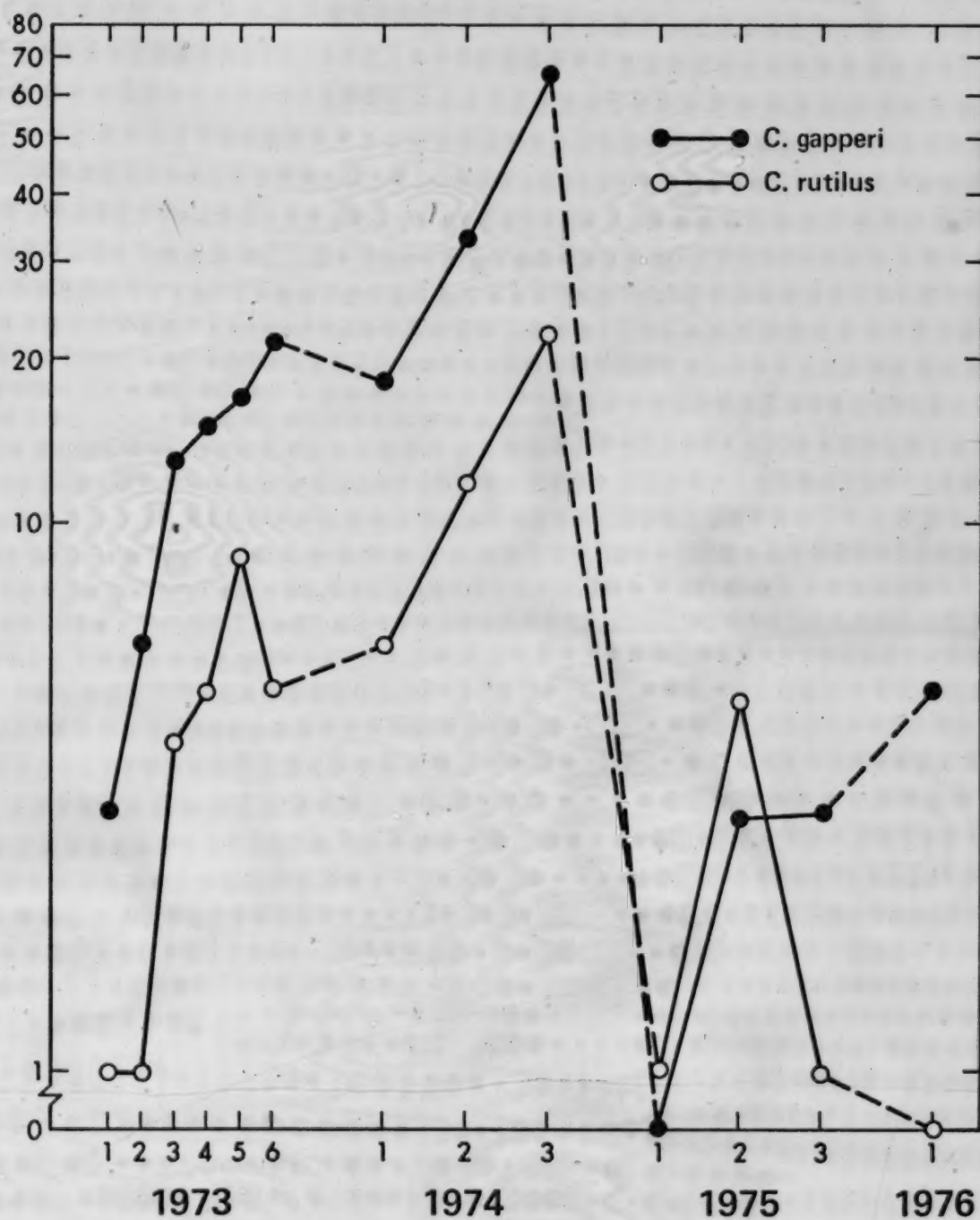
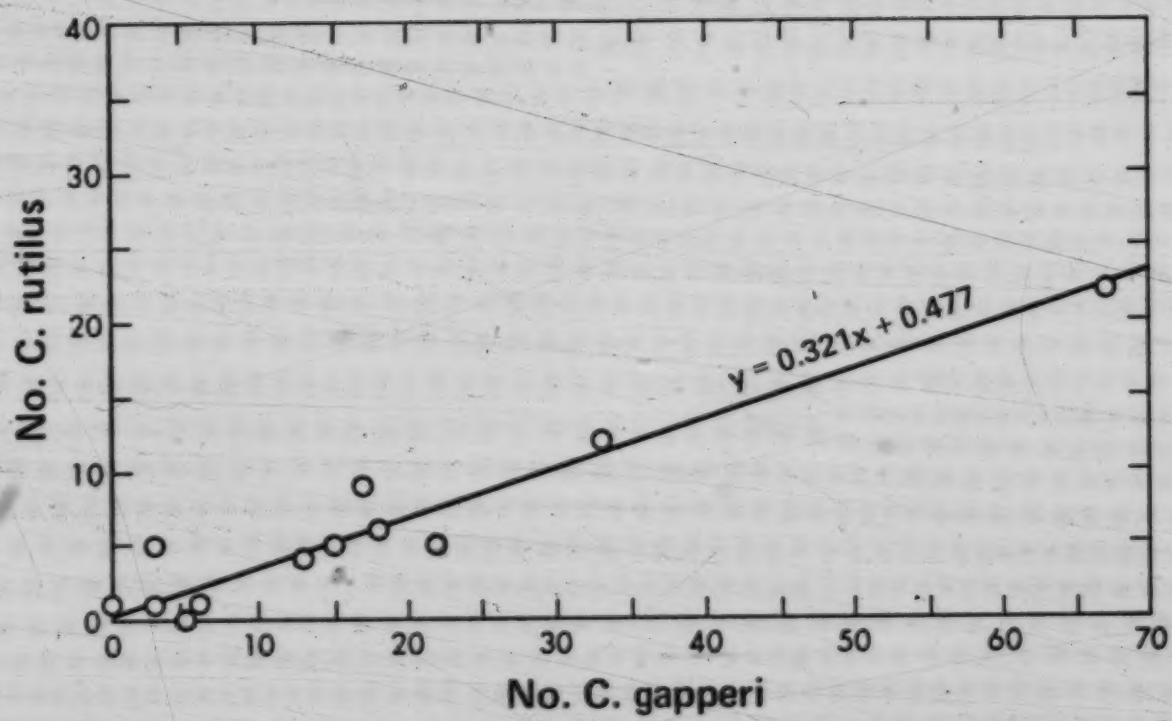


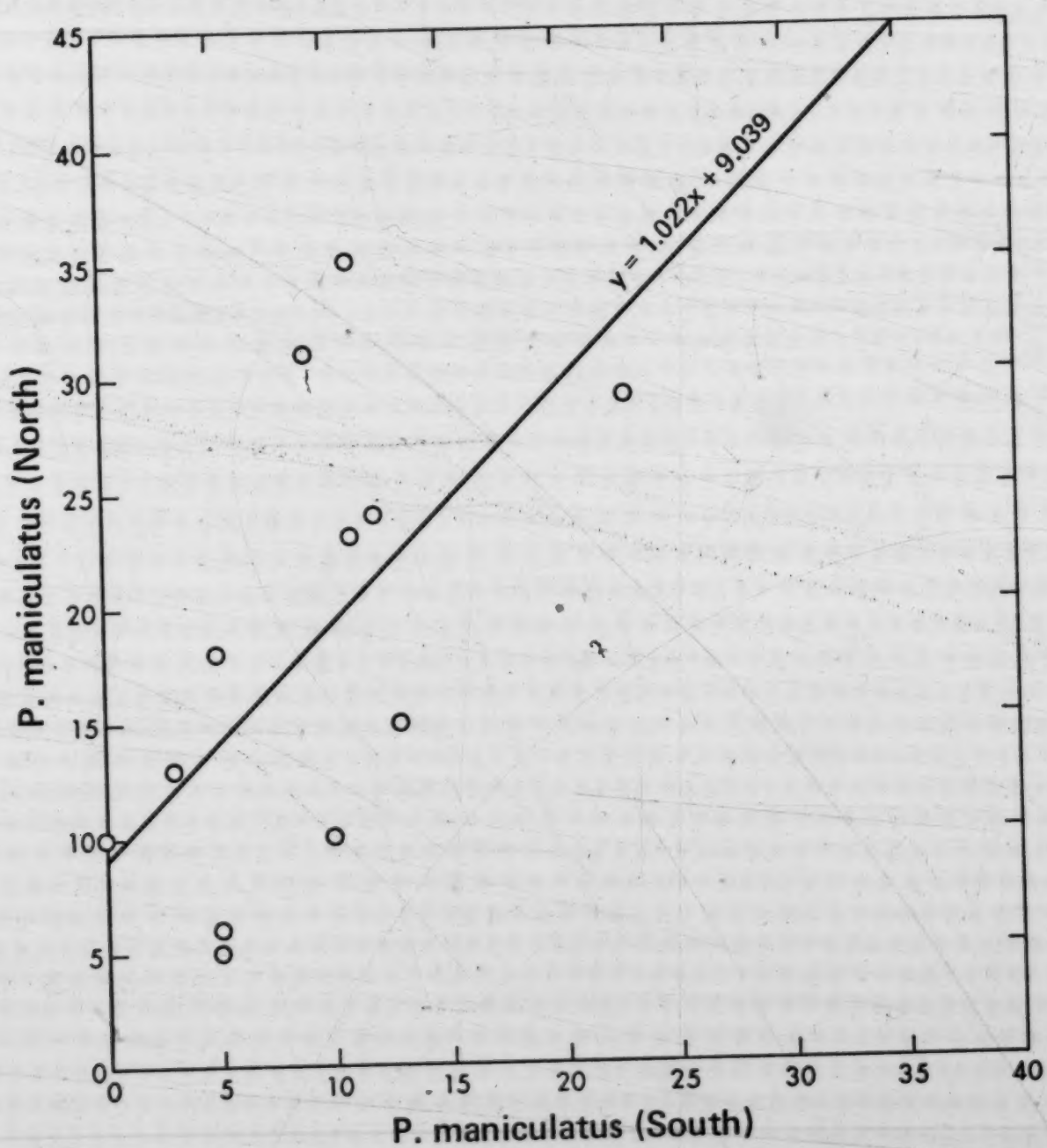
Figure 6. Correlation between crude numbers of Clethrionomys gapperi and C. rutilus per live-trap session, 1973-6.



on each side of this section of the Kakisa River (Day 1968). The south plot is characterised by sloping, well-drained soils which have a high content of stones and loam, with some sand and gravel. These well-drained areas are vegetated by jack pine (Pinus banksiana), white spruce (Picea glauca), aspen (Populus tremuloides) and willow (Salix spp.), and a ground cover of rose (Rosa woodsii), bearberry (Arctostaphylos uva-ursi), Labrador tea (Ledum groenlandicum), lichens, mosses and grass. There are small areas of poor drainage which contain black spruce (Picea mariana), tamarack (Larix laricina), dwarf birch (Betula spp), and juniper (Juniperus horizontalis). By comparison, the north plot is mostly level and poorly drained, with soils that contain loam, sand and, in some localities, peat; stones or gravel do not occur here. These soils tend to support a growth of tamarack, black spruce, dwarf birch and willow, with a ground cover of juniper, Labrador tea, bearberry, Cladonia and sedges. A small part of the plot was composed of well-drained sandy soil on which mature jack pine and white spruce were found, with a sparse ground cover of rose, bearberry, cranberry (Vaccinium vitis-idaea), lichens, mosses and grass.

Densities of Peromyscus on each plot were also correlated, but numbers were slightly higher on the north side (Fig. 7), which might suggest that competition between Peromyscus and Clethrionomys is responsible for the lower

Figure 7. Correlation between crude numbers of Peromyscus
maniculatus on north and south plots per live-
trap session, 1973-6.



densities of C. rutilus. Correlation between Peromyscus numbers from each plot ($r=0.616$, $df = 11$, $p<0.05$) is not as close as that for Clethrionomys ($r = 0.957$, $df = 11$, $p<0.001$), but the slope is much closer to 45° , which indicates that the two populations of Peromyscus attain similar numbers at the peak density. Thus the evidence from Peromyscus on each side of the river suggests that habitat conditions are not as critically different as Clethrionomys might suggest, at least not for Peromyscus.

Allowing for the different densities of Clethrionomys, then, the two populations generally exhibit the same rates of natural increase through each summer and similar rates of decline over each intervening winter. In the latter instance, there are two somewhat anomalous trends, however, where numbers of overwintered animals for C. rutilus in 1973-4 and C. gapperi for 1975-6 appear to increase. Both these increases could well be the result of immigration from the surrounding area or capture of previously undetected juveniles from the late cohorts of the previous summer, in that the difference in numbers between fall and spring in both instances is created by the addition of two or three unmarked individuals.

Population densities of both species were at a moderately low level in 1973, increased to a peak in 1974 and then declined sharply to low densities in 1975. Fuller (1969) has shown that population densities of these two species peaked in 1962 and 1966, with low densities during

the years 1963-5, although they appeared to be out of phase in 1967, when C. rutilus numbers remained relatively high while C. gapperi numbers declined. He also indicated (Fuller 1977 and unpublished data) that populations of both species increased to peak levels during late summer in 1974 and 1976 and, to a lesser extent, in 1970. Thus fluctuations in abundance of C. gapperi and C. rutilus appear to move in synchrony.

While obtaining voles for the behavior studies, I caught a considerable number of pregnant females that I housed in rat-size cages and permitted to raise litters in captivity. The average number of young per litter (Table I) shows no significant difference between species for the two years combined ($t = 0.14$, $df = 48$, $p > 0.1$). Average litter size in both species was larger in 1974, when the vole populations reached peak densities, than in 1975 when population density was considerably lower. I was unable, however, to find a significant difference between the figures for the two years ($t = 1.79$, $df = 48$, $p > 0.05$). The reason for the subgrouping of the figures into litters of overwintered and young-of-the-year females is that age of the female is known to affect litter size (Saint Girons 1971, Fuller, pers. com.).

On the basis of the foregoing considerations, therefore, I can see no obvious differences in the structure

Table I. Mean litter size for litters born to pregnant wild-caught voles and raised in captivity, 1974 and 1975. OW = litters born to overwintered females; J = litters born to females born in the same year; C.G. + C. R. = data pooled for both species, regardless of OW or J. Numbers in parentheses indicate sample size.

YEAR	C. GAPPERI Litter Size	C. RUTILUS Litter Size	C.G. + C. R. Litter Size
1974 (OW) (J)	6.00 $\pm$ 0.52(6) f	5.60 $\pm$ 0.25(5) 7.00 $\pm$ 0.58(3)	6.07 $\pm$ 0.29(14)
1975 (OW) (J)	5.13 $\pm$ 0.35(8) 5.75 $\pm$ 0.25(8)	5.33 $\pm$ 0.69 (9) 5.27 $\pm$ 0.33(11)	5.36 $\pm$ 0.22(36)
1974+ 1975	5.59 $\pm$ 0.22(22)	5.54 $\pm$ 0.27(28)	

and dynamics of the two populations of Clethrionomys at the Kakisa River. There also appears to be no noticeable difference in the reproductive pattern between the two species (Fuller, unpublished data). It is possible that there is a lower density of C. rutilus at the boundary than C. gapperi, although whether or not this is due to the minor habitat differences already noted is difficult to prove. Since Dyke (1971) has already shown that the habitat and food requirements of these species do not differ markedly, the potential for competition between the species at the Kakisa River, must exist.

(2) Distribution of Clethrionomys at the Kakisa River

Intermittent trapping at the Kakisa River over the last sixteen years has demonstrated that the boundary between the species is not inviolable (Table 2). It is not possible to say how long voles have been crossing the river. Contrary to my hypothesis the rate of immigration appears to be equal in each direction, with 2.5% of the south bank population and 3.0% of the north bank population being composed of the inappropriate species. Since the trapping effort was far from equal on each side of the river, it is only possible to compare figures within each population rather than between the populations.

Of the 18 voles which have been taken on the "wrong" side of the river (see next section for confirmation of species), eight (+one possible extra) were overwintered

Table 2. Total numbers of Clethrionomys gapperi and C. rutilus trapped on each side of the Kakisa River, 1961-1976. (Data for the years 1961-1972 and 1976 kindly provided by Dr. W. A. Fuller).

YEAR	SOUTH BANK		NORTH BANK	
	C. GAPPERI	C. RUTILUS	C. GAPPERI	C. RUTILUS
1961	31	3	-	-
1961	60	0	-	-
1963	16	0	-	-
1964	-	-	-	-
1965	1	1	0	2
1966	39	0	0	23
1967	5	0	0	10
1968	2	0	-	-
1969	-	-	-	-
1970	-	-	0	6
1971	-	-	-	-
1972	1	0	1	14
1973	37	0	0	25
1974	141	3	2	100
1975	56	3	2	48
1976	8	0	3	41
TOTAL	397	10	8	269
% TRAPPED ON				
"WRONG" SIDE				
OF RIVER				
	2.5%		3.0%	

animals which could have crossed by traversing frozen river ice during the previous winter (Table 3). The other 9 voles were all young-of-the-year which either must have crossed the river while it was not frozen, or were born on the "wrong" side. While it may seem unlikely that an equal number of animals could cross the swiftly-flowing Kakisa River in the summer as could cross the ice in winter, dispersal is greatest during summer and fall, when population density and reproductive activity are both high, and so pressure to cross the river is at its maximum.

Possibly small breeding groups of each species have become established in the range of the other species. Whether these groups are large enough, or acquire additional recruits at a rapid enough rate to sustain or expand their numbers, or whether they are still being eliminated after a year or two is difficult to assess. On the other hand, it would only take one pregnant female vole crossing the river in summer to introduce 4-6 new individuals into the population of the other species. Two groups of C. rutilus, three trapped in September 1961 and two in May 1974, and three C. gapperi trapped in August 1976 (Table 3), might well be litter-mates. None of the seven adult female voles taken on the "wrong" side of the river were pregnant on capture (or had previously bred, according to autopsy), however, so I am unable to support either claim. Thus data from three years of intensive trapping at this small portion of the boundary of C. gapperi and C. rutilus are

Table 3. Details of all voles caught within the range of the opposite species during the years 1961-76.

(M = male, F = female, OW = overwintered individual, J = individual born the same year of capture; E = east, W = west of Kakisa River).

SPECIES & NUMBER	SEX	WEIGHT (GRAMS)	AGE	DATE OF CAPTURE	LOCATION
CR369	F	19.5	J	2 Sept 1961	Lady Evelyn Falls(E)
CR370	M	19.6	J	" " "	" " " (E)
CR378	F	17.2	J	3 " "	" " " (E)
CR106	M	19.6	J	7 Aug 1965	" " " (E)
CG62	F	21.7	OW	24 June 1972	West mouth of Kakisa
CG110	-	-	OW	10 May 1974	Lady Evelyn Falls(W)
CR32	M	19.5	OW	27 " "	2 km south of camp
CR73	F	28.0	OW?	17 July 1974	Live trap plot(Sth)
CG43	M	15.0	J	28 Aug "	" " " (Nth)
CR115	M	14.5	J	8 Sept "	Kakisa bridge (E)
CR12	F	16.0	OW	8 May 1975	Kakisa bridge (E)
CG41	F	19.0	OW	10 June "	Kakisa Ford (W)
CG43	M	25.5	OW	17 " "	½ km W. Kakisa bridge
CR48	M	22.5	OW	19 " "	Lady Evelyn Falls(E)
CR64	M	20.0	OW	5 July "	Kakisa camp
CG460	M	18.1	J	19 Aug 1976	Kakisa bridge (W)
CG519	M	19.3	J	30 " "	" "
CG521	M	17.8	J	" " "	" "

not sufficient to resolve these questions.

(3) Confirmation of Species

During the course of my study at the Kakisa River, I trapped 232 voles and obtained an additional 11 voles from Heart Lake and 12 voles from Fort Providence. For full details of individual characters of each vole, see Appendix 1. I assigned all individuals initially to one or other species on the basis of pelage coloration alone, and was impressed by the degree of definition which appeared to exist between the species at this common boundary.

While I feel a reasonable degree of confidence in my own visual identification of individual voles, however, I acknowledge that within the geographic range of each species, considerable variation in pelage coloration does exist (Hall and Kelson 1959). Bolshakov (1962) also noted a great degree of variation in pelage coloration in C. rutilus and C. glareolus, and observed that there was a distinct clinal trend in the variation. Nevertheless, he was able to attribute individual C. rutilus captured in neighboring territories, to different subspecies on the basis of color alone (Bolshakov 1963).

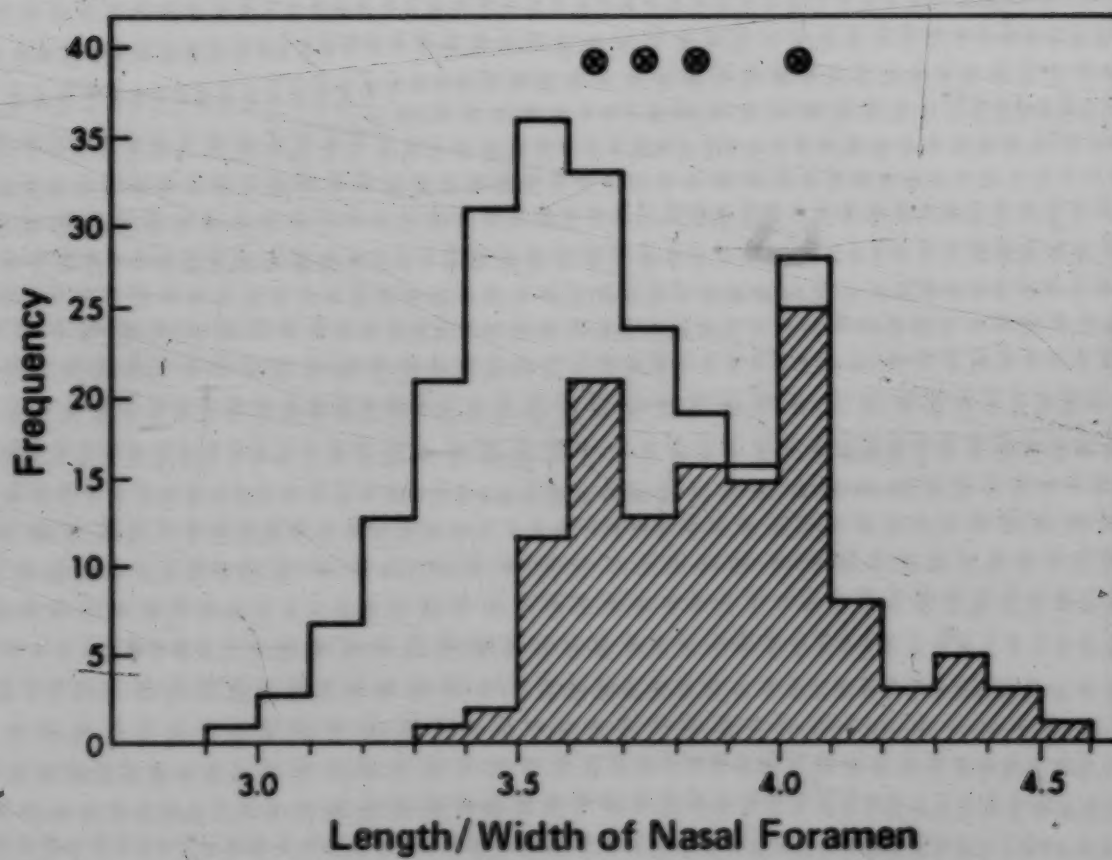
Taxonomically, the source of species distinction in mammals has resided in a few described skull characters. In these two species of Clethrionomys, the single most reliable character of species identification is the condition of the post-palatal bridge, which is complete in C. gapperi and incomplete in C. rutilus (Hall and Kelson ibid). Even this

characteristic is not absolute in defining the species, however, since extremely old C. rutilus or very young C. gapperi may occasionally display post-palatal features normally ascribed to the other species.

Another skull feature which enables a certain degree of specific identification is the shape of the nasal foramen. In C. rutilus, the foramen tends to be somewhat "pear-shaped" as compared to the more "rod-shaped" foramen of C. gapperi, such that the ratio of length to width of the foramen is lower for the former than the latter. Since this feature exhibits a considerable amount of variation in voles of all ages, the segregation of the two species is far from complete (Figure 8). Such overlap cannot be ascribed to hybridization or genetic introgression, since individuals trapped at Heart Lake and Fort Providence, some 50 km from the common boundary and thus well within the range of each species, also showed a similar overlap in nasal foramen dimensions. However, in the few cases where species identification was dubious according to pelage coloration or condition of the post-palatal bridge, the length/width ratio of the nasal foramen provided a useful supplementary measure. Only areas of the histogram where there was less than 10% overlap with the other species were accepted for designation of species when the other criteria failed, so that the maximum value for C. rutilus was 3.59 and the minimum value for C. gapperi was 3.80.

Of the 232 voles trapped at the Kakisa River, I examined the skull features of 184 individuals (90 C. gapperi and 94 C. rutilus, as assigned by pelage). Eighty-eight of the 90

Figure 8. Distribution of the ratios of the length/
width of the nasal foramen of specimens of
C. gapperi (hatched area) and C. rutilus
(open area). Four point above histogram =
gapperi/rutilus hybrids.



C. gapperi possessed complete post-palatal bridges and 87 of the 94 C. rutilus had incomplete post-palatal bridges. One of the two aberrant C. gapperi was a very young individual (less than one month old) in which the sutures of the post-palatal bridge had not fused yet; unfortunately, I did not obtain any information on the nasal foramen, although the vole was probably a C. gapperi. The other questionable C. gapperi possessed a "rutilus-red" pelage, a post-palatal bridge that was incomplete on one side and fused on the other, and nasal foramina which were indeterminate in character. Furthermore, this individual was captured in the same area at the same time as a confirmed C. rutilus individual (on the "wrong" side of the river), so was most probably a hybrid. This contention is further supported by the discovery in the same area of an individual C. gapperi, confirmed by the complete post-palatal bridge, which also exhibited a "rutilus-red" pelage. Thus there were two possible hybrids obtained from the C. gapperi side of the Kakisa River.

Voies from the C. rutilus side of the river included 7 individuals possessing complete post-palatal bridges, of which 4 were old individuals (at least 12 months old) and so had probably possessed incomplete bridges earlier in life. All 4 were certainly "rutilus-red" in appearance and possessed nasal foramen ratios that fell within the C. rutilus range. Of the other three, one vole had the appropriate red pelage and nasal foramen, but the other two possessed indeterminate foramina. One of these two was a female which, being pregnant

on capture, subsequently raised a litter of seven. All the young appeared to be "rutilus-red" and, of the four skulls which were kept, all possessed incomplete post-palatal bridges, while two of the four exhibited indeterminate nasal foramina. Thus there appeared to be three possible hybrids in the population inhabiting the C. rutilus side of the river.

Frustration with the problem of designation of these, and other, species on purely morphological grounds has generated the recent surge of interest in biochemical taxonomy. Despite development of more refined techniques, however, characterisation of the species which comprise the genus Clethrionomys has remained relatively intractable (Johnson 1968). Canham and Cameron (1972) demonstrated that in the vicinity of the Kakisa River, C. gapperi was homozygous for either transferrins M or J, or heterozygous for both, with approximately equal frequencies, whereas 98% of the C. rutilus population was homozygous for transferrin M, and 2% heterozygous for transferrins M and K. Albumin G was found in 90% of C. gapperi and 6% of C. rutilus, while albumin P was found in the remaining 94% of C. rutilus only, and albumin M in 10% of C. gapperi. Thus it is theoretically possible to assign individuals to one or other of the two species on the basis of transferrins and albumins alone.

I only obtained blood samples from 101 of the 232 voles, since this included snap-trapped animals, live-trapped animals that died during or shortly after confinement, or died

during subsequent breeding trials, before blood could be obtained. Unfortunately, I found a certain amount of variation in the actual distances migrated by the transferrins. Since transferrin bands M, K and J are known to migrate distances of 48, 51 and 53 relative to albumin G distance 100 (Canham and Cameron ibid), occurrence of a number of individual samples with one or two bands having migration values ranging from 45 to 56 meant that I was unable to confirm the identity of transferrins. Also, I could not assume that all heterozygous individuals were most probably C. gapperi, since I found a greater frequency of heterozygosity in C. rutilus than Canham and Cameron (ibid) noted (4 out of 32 heterozygous, i.e. 13% compared to 2%, or less, previously reported). Thus the technique of electrophoresis and measurement of migration rates of serum proteins does not appear to be a very reliable tool for assigning individuals to one species or the other at the Kakisa River.

The occurrence of more heterozygotes than expected in the population on the C. rutilus side of the river is of great interest. Since frequency of heterozygosity in the C. rutilus population north of the common boundary on the Alaska highway was as high as 12% (Canham and Cameron ibid), the higher value could be due to natural variation within the population. However, it could well be that a certain degree of genetic "leakage" may be occurring at the Kakisa River, such that genes governing heterozygosity in C. gapperi could

be appearing in the C. rutilus population. Of the four heterozygous C. rutilus-types, two had appropriate pelage, post-palatal bridge and nasal foramen characters. One individual had C. rutilus-type pelage and nasal foramen, but possessed a complete post-palatal bridge, which may indicate hybridization. The fourth vole was C. rutilus-like in all three characters, although it was captured on the C. gapperi side of the river. The display of heterozygosity may not necessarily be limited to the F1 generation, but may indicate the reoccurrence of characters acquired from the crossing of species-true types in earlier generations. This is supported by data on relative frequencies of α -globulins, which differ markedly across the species' range, but are strikingly similar in both species at the common boundary (Canham and Cameron ibid).

The four individuals which comprised the single cross-bred litter raised in captivity present an interesting combination of the two species' features. The pelage coloration in all four was generally "rutillus-red" on the back and ears, but the tail was not characteristically orange or as thick as the rutillus type. The post-palatal bridge was incompletely formed in all four, a distinctly rutillus-like feature. However, the serum proteins indicated that all four were heterozygous for transferrins. Dimensions of the nasal foramen distributed the four individuals evenly from predominantly rutillus-like to predominantly gapperi-

like (Figure 8), although no single vole was clearly indicative of one species or the other. Thus the hybrid voles appeared to comprise a mixture of the features of the two species.

The evidence I have presented indicates that 95% of the voles trapped at the Kakisa River were readily assigned to one or other of the two species on the basis of pelage coloration and post-palatal bridge alone. This includes the seven voles trapped on the "wrong" side of the river which were assigned to species by all three morphological characters. The remaining 5%, comprising 9 voles, could not be readily assigned and appeared to include at least five possible hybrids. If I add to these the one confirmed C. rutilus from the C. gapperi side of the river, as mentioned above, I end up with at least 6, and possibly 10, of the total of 184 voles as possible hybrids. Thus 3-5% of the populations either side of the Kakisa River appear to be composed of hybrid individuals.

(4) Aspects of Reproductive Isolation in Clethrionomys

(a) Copulatory Behavior

A summary of my observations of the copulatory behavior of the two species is given in Table 4. Although two experimental sessions were run, which would have resulted in two of each type of possible pairing, a female C. gapperi instead of C. rutilus was mistakenly placed with a male C. gapperi so that three C. gapperi x C. gapperi

Table 4. Summary of copulatory behavior of voles in species-true and cross-specific pairings per 8-hour observation period. All copulations were observed during the first 4-hour section of the observation period. No litters were produced by any of the mated females.

VOLE PAIRS		MINUTES ACTIVE		MINUTES ACTIVE TOGETHER	MINUTES TO FIRST COPULATION	TOTAL NO. OF COPULATIONS	COPULATION FREQUENCY (C/MINUTE)
M	F	M	F				
C.G.	C.G.	210	110	95	95	9	0.09
C.G.	C.G.	250	165	160	40	32	0.20
C.G.	C.G.	75	120	15	-	0	-
C.R.	C.R.	90	20	15	-	0	-
C.R.	C.R.	155	65	25	-	0	-
C.G.	C.R.	245	60	60	130	15	0.25
C.R.	C.G.	150	100	40	-	0	-
C.R.	C.G.	115	135	80	15	14	0.18

trials were run and only one trial of male C. gapperi x female C. rutilus. Nevertheless, certain information emerges from even this low number of trials.

First of all, there is a large amount of variation in the amount of time that voles were active and the amount of time that they spent together. Second, not all pairings resulted in copulation; notably, the species-true pairs of C. rutilus did not attempt to copulate at all during eight hours of observation. This is not to say, of course, that they did not copulate during the nine-hour overnight period between observations.

For cross-specific pairs, two out of three trials yielded copulatory behavior, the same as occurred for C. gapperi x C. gapperi. What is more, frequency of copulation in the two trial conditions is of the same order. Thus individual voles did not seem to behave any differently towards the mate as far as reproductive behavior was concerned, regardless of species.

I do not feel that this necessarily means that there is no segregation between these species reproductively. Certainly, I did not see any difference in the repertoire of behavior exhibited by male voles in approaching a female, nor in the subsequent responses of the female to the mating attempts of the male, in any of the three types of species combinations where mating was observed. None of the mated females produced any litters however, even

though copulation appeared to be successful. Dewsbury (1975) has shown that although copulation between two species of Peromyscus was possible, differences in actual copulatory techniques ensured that no successful insemination occurred. It could well be that segregation in these two species of Clethrionomys is achieved in a similar manner, although I have no evidence to either support or refute such a claim.

(b) Breeding Trials

I conducted a total of 108 breeding trials using adult wild-caught voles during the winter of 1973-4 and the summers of 1974 and 1975. The breeding success in species-true pairings was 14% and 41% compared with 1% in cross-specific pairs (Table 5). The single litter raised as a result of cross-breeding between a male C. rutilus and a female C. gapperi comprised one male and three females, and back-crossing with parental stock demonstrated that at least the male individual was fertile when crossed with a female C. gapperi. These cross-bred individuals were somewhat "rutilus-like" in external features although skull features were intermediate in character (see section on "Confirmation of Species"). I also noticed that individuals in the hybrid litter were very aggressive toward one another, a phenomenon which Godfrey (1958) noted in hybrids produced from inter-racial crossing in C. glareolus.

The low level of species-true breeding might well be a result of stress induced by confinement, although one would naturally expect similar effects in cross-specific

Table 5. Summary of breeding trials conducted in Edmonton, 1973-4 and at the Kakisa River, Northwest Territories, 1974 and 1975.

	<u>GAPPERI/ GAPPERI</u>	<u>RUTILUS/ RUTILUS</u>	<u>GAPPERI/ RUTILUS</u>
No. PAIRINGS (P)	14	17	77
No. LITTERS (L)	2	7	1
L/P	0.14	0.41	0.01
No. LITTER SIZES			
1	0	1	0
2	0	0	0
3	0	0	0
4	1	2	1
5	0	1	0
6	1	1	0
7	0	1	0
MEAN LITTER SIZE:	5.0	4.5	4.0

breeding. I have observed several wild-caught pregnant females abort their litters or consume them shortly after giving birth; thus it seems that certain individuals do not exhibit normal reproductive activity in confinement. Since I did not provide voles with fresh green food (such as barley sprouts) in breeding trials during the summers of 1974 and 1975, it is possible that voles lacked certain nutrients in their diet essential for the maintenance of reproductive condition (Batzli and Pitelka 1971). Another point is that I only caged voles together for 2 weeks, which might not have been long enough for some pairs to breed. A further point is that voles are most susceptible to becoming pregnant again a few days after giving birth and, since I did not have large enough cages to enable a male vole plus a female with young to live in close proximity without severe fighting, I probably missed the optimum time for breeding in every case. Finally, it has been noted that while C. glareolus is an induced ovulator, pregnancy is easily blocked by the exposure of females to strange males (Clarke et al. 1970); perhaps breeding in some female C. gapperi was suppressed in a similar fashion.

It should not be assumed that 100% breeding success is possible in Clethrionomys in the laboratory; Saint Girons (1972) demonstrated that reproductive success in laboratory bred C. glareolus was significantly lower than in wild-bred animals. Grant (1974) found that even when species-true

pairs of C. gapperi and C. glareolus were set up for 1-12 months, only 50% breeding success was obtained. Morrison et al. (1976) also only obtained 46% breeding success with C. rutilus continuously caged together in breeding pairs in the laboratory. Reproductive success of C. gapperi in my own breeding trials was somewhat lower than that of C. rutilus. Murie and Dickinson (1973) and I have shown that in captivity C. gapperi is much more active than C. rutilus (see section entitled "Behavior Experiments"). Such activeness, and possibly aggressiveness, in caged C. gapperi could well reduce the reproductive success compared to the less perturbable C. rutilus; such maternal aggressiveness has been shown to reduce litter-raising success in Peromyscus (Savidge 1974). A similar situation has been observed in C. glareolus, in which island subspecies were found to be much more docile than their mainland counterparts (Steven 1953, Godfr y 1958).

No cross-breeding was achieved during winter trials in Edmonton. Among species-true breeding pairs, however, a litter was raised from a C. rutilus from Kakisa and one from Inuvik, which indicates that breeding is possible across the geographic range of one of the species at least, even if it is extremely limited between species at the boundary.

Of 118 cross-specific and 53 species-true breeding

AD trials using voles from litters born to pregnant wild-caught females, conducted at Heart Lake during the winter of 1974-5, only one species-true litter was produced. The overall lack of breeding in these voles was probably due to a failure to attain sexual maturity before winter came on. In spite of providing high-protein chow and increasing light and temperature, conditions were not sufficiently controlled to induce breeding. I also noticed that many of these voles were extremely active, which would make them even less amenable to caging and breeding than wild-caught voles. There certainly seemed to be a higher mortality of these voles when they were in pairs than was seen in any of the other breeding trials. For these reasons, then, I have not included these figures in the results.

J Thus there is very low incidence of cross-breeding in captivity and, according to my identifications to species, in the wild. However, it is more important to consider reproductive isolation in terms of gene flow and not in terms of interbreeding (Bigelow 1965), as selection will inhibit gene flow between two differently well-integrated gene pools despite interbreeding. Therefore a small amount of cross-breeding between C. gapperi and C. rutilus is unlikely to lead to any reduction in specific integrity at the Kakisa River. Even when there are no barriers to dispersal, and overlap of species' ranges occurs, such as

that found in subspecies of mole rat, Spalax ehrenbergi, (Nevo and Bar-El 1976) and in subspecies of pocket gopher, Thomomys talpoides, (Nevo et al. 1974), selection against hybrids in terms of cytogenetic, ethologic and ecological incompatibilities has resulted in very narrow hybrid zones and has ensured maintenance of species identity.

Demonstration of almost complete reproductive compatibility between C. gapperi and C. glareolus (Grant 1974) would seem to run counter to the arguments above, particularly considering that these two species were separated by thousands of miles for many thousands of years (Rausch 1963). It could be assumed that C. gapperi and C. rutilus, now in close geographic proximity and probably separated for a shorter period of time than C. gapperi and C. glareolus, would easily interbreed and thus be regarded as sibling species. That reproductive isolation is less developed in C. gapperi and C. glareolus is reasonable if one accepts that they have responded to similar environmental pressures while geographically isolated in Eurasia and North America, so that reproductive isolation would only develop by chance (Nadler et al. 1976). On the other hand C. rutilus, having possibly diverged from gapperi-glareolus ancestral stock, is more of a tundra-dwelling species than C. gapperi and C. gapperi and C. rutilus have had more recent contact than C. gapperi and C. glareolus. In short, adaptation to different habitats and a background of geographic con-

tact have combined to produce a more rapid evolutionary divergence between C. gapperi and C. rutilus (Nadler ibid).

(5) Mobility of Clethrionomys in the Field

I have hypothesized that there are differing levels of mobility in the two species of Clethrionomys which result in a greater tendency for the more mobile species to migrate across the Kakisa River. Is there any indication from the live-trap data that mobility is any different between the species? Although the mean distance travelled between traps by C. gapperi appears to be greater than that exhibited by C. rutilus, the difference is not statistically significant (Table 6). Because of the paucity of data on C. rutilus, however, one cannot accept or reject the possibility of differences in the movement of voles between traps. Of the seven combinations tested (LOW NOS: Cg male vs. Cr male, Cg female vs. Cr female, Cg male vs. Cg female, Cr male vs. Cr female; HIGH NOS: Cg male vs Cg female; Cg male low vs. high; Cg female low vs high) the only figures which showed significant differences were between low density C. gapperi males and females ($t = 2.00$, $df = 51$, $p < 0.05$) and C. gapperi males at low and high densities ($t = 3.12$, $df = 46$, $p < 0.01$). These differences agree with findings of other workers that females tend to occupy smaller home ranges compared to males (Brown 1969,

Table 6. Mean inter-trap distances for voles captured on the east and west sides of the Kakisa River, 1973-5, segregated according to low (< 10 voles/hectare), medium (10-20 voles/ha.) and high (> 20 voles/ha.) population densities. Numbers in parentheses indicate sample size.

	<u>C. GAPPERI</u>	<u>C. RUTILUS</u>
<u>MALES</u>		
LOW DENSITY	36.58 ± 4.97 (23)	30.90 ± 6.77 (11)
MEDIUM DENSITY	25.01 ± 4.67 (20)	-
HIGH DENSITY	19.02 ± 2.85 (25)	-
<u>FEMALES</u>		
LOW DENSITY	24.10 ± 3.55 (20)	20.87 ± 7.92 (10)
MEDIUM DENSITY	22.19 ± 2.90 (18)	-
HIGH DENSITY	18.64 ± 2.61 (17)	-

Mazurkiewicz 1971, Herman 1975, Wells 1976), and that as population density increases, individual vole movement is decreased (Andrzejewski 1967, Watts 1970b).

mobility and the similar proportions of each species in the population of the other, there appears to be little support for the hypothesis of unequal migration across the Kakisa River. In the next section, I will deal with the large differences in levels of activity, and other aspects of behavior, which were readily apparent in the pen experiments. Whether such differences in activity in the pen indicate a real difference in the behavior of the two species in the wild, however, remains open to speculation.

(6) Behavior Experiments

(a) General Remarks

Observations on 72 male voles in the different species combinations and 36 female voles in species-true combinations occupied 288 hours. From these observations I calculated distance moved, length of time active, distance/time ratio and number of wins, losses and neutral outcomes to the encounters for each individual (for details see Appendix 2). I noticed that there is a high degree of individual variation between voles, with distances covered ranging from 22 m to 1722 m, time active from 13 minutes to 287 minutes and number of encounters ranging from 0 to 76 in the 8-hour observation period.

As the latter figures indicate, there were far fewer interactions, especially aggressive encounters, observed in this study compared to similar studies of these species using smaller arenas (Johst 1967, Grant 1970a, Murie and Dickinson 1973, Mihok 1976). Neutral encounters consisting mainly of mutual avoidance, which Brown (1964) described as a means of reducing aggression between species, appear to make up the greatest proportion of interactions observed. Not only does aggression seem to be reduced by an increase in arena size (Poole and Morgan 1976), but it is also affected by the complexity of the arena, i.e. by the provision of moss, logs, nest-boxes and feeders, such that fighting and chasing are both greatly reduced (Crowcroft and Rowe 1963).

Thus one is caught between the problem of unrealistically high levels of aggression resulting from artificially small and simple arena situations, and the problem of too few encounters due to a large and complex pen which more closely resembles the natural situation. I feel that I have leaned towards the latter. Having allowed for these problems, it still seems that aggressive interactions are not common in these species in the wild and are probably not as important in population regulation as suggested for other species of voles (Chitty 1960, Krebs 1970).

In the following sections, I will examine various aspects of the behavior of Clethrionomys gapperi and C.

rutilus.

(b) Brief Description of Clethrionomys Behavior

After introduction to the runway, each vole ran immediately into one or other of the two pens, the longest time taken to enter a pen being two minutes. Initial pen selection appeared to be entirely random and, within each trial, selection by first and second voles did not affect choice of pen by second and third voles. Once in the pens, voles proceeded to explore actively, moving in a short, jerky gait with ears forward and tail raised, in an attentive manner such as described for Microtus (Clarke 1956). For the first 30 minutes or so, voles were in a "hypersensitive" state, and the slightest noise or encounter with, or sight of, another vole would send them scurrying for the cover of a log or nestbox. At this time there was usually a great deal of "rooting" in the moss covering the pen floor, by digging with forepaws, nasal investigation and tunneling, such that the whole animal often disappeared from view for a period of time. This facility for burrowing and hiding from view seemed to be extremely important to voles in their process of "settling down", and also reduced the incidence of encounters, as a vole in a moss pile would frequently be overlooked by another exploring vole.

At no time could I discern any difference in patterns of behavior in the two species; manner of exploration, approach, and encounters (including aggression, when it

occurred) were the same as that described by Johst (1967), Skirrow (1969) and Mihok (1976). There was, however, a considerable difference in the quantitative aspect of behavior (see section on analysis of activity levels). Also, since I used a larger area than commonly employed in open-field experiments and observed the voles from a greater distance (about 4 m), I did not see some of the more detailed aspects of interactions. Behavioral characters that I did not see, but which have been described for C. gapperi (Mihok 1976), were the stretch posture (after Johst ibid), naso-anal investigation (except in the male-female pairs of voles in the copulatory behavior trials), raising of front paw only or whole front of body (after Johst ibid), groom other vole, huddle with other vole and pawbeating of opponent. Vocalizing was infrequent and, when it did occur, it was impossible to tell which vole had emitted the sound; thus, although vocalizing may be associated with aggression (Turner and Iverson 1973), it was not included in the following analysis.

Components of behavior that I did see included exploration, escape moves (leaping up at pen walls), sitting still, approach, stare, attack, chase, flee, avoid, ignore other vole, retaliate (aggressive response of vole to attack by dominant), self-groom, nest-build and scent-mark (see next section). The attack component was similar to that described by Colvin (1973) and what Skirrow (1969)

called "lunge", but also included what others termed "fighting" (Clarke 1956, Krebs 1970, and Colvin 1973), simply because fights occurred too infrequently to warrant separate classification. Chase differed from attack in that no physical contact was made and one vole fled while the other followed for a considerable distance at full speed. Therefore only a small number of behavioral components were analysed, since many did not occur sufficiently frequently to warrant attention. One exception was scent-marking which, although observed relatively infrequently, is probably of considerable importance in the interspecific and intraspecific interactions of voles in the wild.

(c) Scent-Marking Behavior

Much attention has recently been devoted to olfactory communication, especially scent-marking, in mammals (Johnson 1973), and more particularly in rodents (Bronson 1971). Although the specificity of what were originally described as mammalian pheromones has been questioned (Beauchamp et al. 1976), there is no doubt that olfaction plays an important role in rodent behavior (Lee 1976, Richmond and Stehn 1976).

The effects of olfactory stimulation on various aspects of rodent behavior have been extensively studied in laboratory mice, with respect to aggression (Archer 1968, Ropartz 1968, Jones and Nowell 1973a), exploratory behavior (Jones

and Nowell 1973b and 1977) and male/female social behavior (Dixon and Mackintosh 1971, Davies and Bellamy 1974) and, in Microtus, with respect to trap response in the field (Boonstra and Krebs 1976). Very little investigation of olfactory communication in Clethrionomys has been done, however. Godfrey (1958) demonstrated that individual C. glareolus were able to discriminate between voles from their population and those from neighboring populations by scent alone. Skirrow (1969) and Skirrow and Rysan (1976) described scent marking in C. gapperi, and Clarke (1956) observed similar behavior in Microtus agrestis, but termed it "displacement digging". Skirrow (1969) noted that Clarke's description of "displacement digging" in M. agrestis almost exactly matched that for scent-marking in M. pennsylvanicus, and so concluded that similar behavior in C. gapperi also constituted scent-marking. Johst (1967) also described marking behavior in several species of Clethrionomys, including C. rutilus, but like Clarke regarded it as a form of displacement activity. Thus scent-marking, and its association with dominance and aggression, could be of importance in the inter- and intra-specific behavior of C. gapperi and C. rutilus (see section on index of aggression).

While I observed scent-marking by voles at the Kakisa River, the incidence was much lower than that in C. gapperi in the central part of its range (Skirrow 1969), 21 of the

72 male voles engaging in scent-marking activity (14 C. gapperi and seven C. rutilus). The greatest number of markings observed for a single vole during an 8-hour observation period was 12, with C. rutilus exhibiting a lower frequency of marking than C. gapperi, although the difference was not significantly different (C. gapperi = 1.94 ± 0.54 , $n = 36$; C. rutilus = 0.72 ± 0.33 , $n = 36$; $t = 1.93$, $df = 70$, $p > 0.05$). Mihok (1976) also noted that scent-marking was less frequent in C. gapperi at Heart Lake (50 km east of the Kakisa River) compared to Skirrow's (1969) findings. As in this study, Mihok did not observe flank-scratching as described by Skirrow (1969), even though Clethrionomys are known to possess flank glands (Quay 1968, Mihok 1976).

(d) Analysis of Activity Levels

In spite of the high degree of individual variation, there are notable differences in levels of activity between the groups of voles according to the species combinations (Table 7). Using Duncan's multiple range test, I calculated significance of differences in activity of the two species in the different triplets, for both males and females, according to distance moved, time active and ratio of distance to time (Table 8). Level of activity of females is considerably lower than that of males, although since activity is much lower in C. rutilus in general, the levels are not significantly different in the one species.

Table 7. Mean ($\pm$ S.E.) distance moved in metres, length of time active in minutes and distance/time ratio per 8-hour observation period, according to the species combinations involved (C.G. = Clethrionomys gapperi, C. R. = C. rutilus). For females, only species-true triplets were used in the pens. Numbers in parentheses indicate sample size.

COMBINATIONS OF SPECIES 6 trials of each) C.G. C.R.	MEAN DISTANCE MOVED/VOLE	MEAN TIME ACTIVE/VOLE	MEAN DISTANCE/TIME RATIO/ VOLE	
	C.G.	C.R.	C.G.	C.R.
MALES				
3 0	1055 $\pm$ 126 (18)	-	184 $\pm$ 12 (18)	-
2 1	565 $\pm$ 108 (12)	281 $\pm$ 68 (6)	135 $\pm$ 14 (12)	90 $\pm$ 14 (6)
1 2	725 $\pm$ 233 (6)	311 $\pm$ 42 (12)	154 $\pm$ 33 (6)	89 $\pm$ 9 (12)
0 3	-	229 $\pm$ 28 (18)	-	67 $\pm$ 6 (18)
FEMALES				
3 0	324 $\pm$ 54 (18)	-	104 $\pm$ 11 (18)	-
0 3	-	135 $\pm$ 32 (18)	-	45 $\pm$ 19 (18)
			2.90 $\pm$ 0.27 (18)	-
			-	2.64 $\pm$ 0.30 (18)

These observations agree with the differences in mobility of voles at low densities in the wild.

Examination of mean figures for distance moved and time active for voles in different species combinations shows that C. gapperi activity is reduced in the presence of C. rutilus, whereas the activity of C. rutilus appears to be increased somewhat in the presence of C. gapperi (Table 7). Because of the different number of voles within each trial situation and the greater degree of variance which this causes, I have combined figures for the two interspecific trials such that three situations comprising 18 voles each are compared; species-true C. gapperi, species-true C. rutilus and a combination of the two species (Table 8b). From this it is evident that activity of male C. gapperi is significantly lower in the presence of C. rutilus than activity in species-true trials, and that both these figures are significantly greater than C. rutilus in species-true or combined trials. C. rutilus, on the other hand, does not show any significant difference in levels of activity either in species-true or combined-species trials. Although there is a good correlation between distance moved and time active for pooled data on the two species (C. gapperi $r = 0.89$, $N = 36$; C. rutilus $r = 0.85$, $N = 36$; $p < 0.01$), there is a large amount of individual variation in the two measures such that distance-time ratios are less sensitive measures of relative activity

in different trial conditions than distance or time on their own (Table 8).

There are two further measures of activity in Clethrionomys which I was able to make. The first I obtained by pooling all encounters (wins, losses and neutral) for each species in the four trial combinations (Table 9). The other measure I made was a calculation of mean number of moves between pens for each species in the four trial combinations (Table 10). Once again, the number of encounters and moves between pens was greatest for male C. gapperi in species-true combinations, both figures being approximately ten times that for C. rutilus in species-true combinations. Accordingly, the former figures were significantly different from all the others when tested by Duncan's multiple range test, and even the fewer numbers of encounters for C. gapperi in interspecific trials were significantly greater than those for C. rutilus in species-true trials (Table 11). C. gapperi males exhibited a greater number of moves between pens in species-true than in mixed-species trials, and, when mixed-species figures are pooled, male C. gapperi exhibit significantly more moves between pens than C. rutilus, regardless of trial conditions. As with other measures of activity, C. rutilus showed no significant difference between groups.

In considering the various measures of activity, it could be construed that many of them were strongly corre-

Table 9. Mean ($\pm$ S.E.) number of encounters per vole per 8-hour observation period according to species combinations involved (C.G. = Clethrionomys gapperi, C.R. = C. rutilus). For females, only species-true triplets were used. Numbers in parentheses indicate sample size.

COMBINATIONS OF SPECIES (6 trials of each)			MEAN NUMBERS OF ENCOUNTERS/VOLE/TRIAL			MEAN TOTAL ENCOUNTERS/ SPECIES COMBINATION
C. G.	C. R.	C. G. x C. G.	C. G. x C. R.	C. R. x C. R.		
MALES						
3	0	24.9 ± 2.5(18)	-	-	74.7 ± 11.1 (6)	
2	1	12.2 ± 3.6 (6)	8.4 ± 1.8(12)	-	29.0 ± 5.3 (6)	
1	2	-	9.8 ± 2.0(12)	6.7 ± 1.8(6)	26.2 ± 5.1 (6)	
0	3	-	-	2.5 ± 0.5(18)	7.5 ± 2.0 (6)	
FEMALES						
3	0	9.5 ± 1.5(18)	-	-	28.5 ± 4.3 (6)	
0	3	-	-	2.1 ± 0.6(18)	6.2 ± 2.3 (6)	

Table 10. Mean ($\pm$ S.E.) number of moves between pens per vole per 8-hour observation period, according to species combination involved. For inter-specific trials, mean pooled figures for each species are also given. Numbers in parentheses indicate sample size.

COMBINATIONS OF SPECIES (6 trials of each)		NUMBER OF MOVES BETWEEN PENS	
CG	CR	<u>C. GAPPERI</u>	<u>C. RUTILUS</u>
MALES			
3	0	60.1 $\pm$ 8.3 (18)	-
2	1	27.6 $\pm$ 8.5 (12)	9.5 $\pm$ 4.3 (6) 12.2 $\pm$ 2.3 (12) 7.5 $\pm$ 1.6 (18) 11.3 $\pm$ 2.1 (18)
1	2	40.3 $\pm$ 16.4 (6)	
0	3	-	
FEMALES			
3	0	12.1 $\pm$ 2.9 (18)	-
0	3	-	3.7 $\pm$ 1.1 (18)

Table 11. Significance of differences according to Duncan's multiple range test between (1) mean number of encounters per pair of voles and (2) mean number of moves between pens per vole per 8-hour observation period. Vole classes joined by a line are not different at the $p < 0.05$ level of significance. (CG = C. gapperi, CR = C. rutilus; tables (a) include data from all possible combinations of voles, tables (b) show pooling of interspecific figures from trials comprising 2CG1CR and 1CG2CR for encounters and intraspecific figures for moves between pens).

(1) ENCOUNTERS

(a) 3CR 3CR CRxCR CGxCR 3CG CGxCR CGxCG 3CG
(F) (M) (1CG2CR) (2CG1CR) (F) (1CG2CR) (2CG1CR) (M)

(b) 3CR 3CR CRxCR CGxCR 3CG CGxCG 3CG
(F) (M) (1CG2CR) (ALL) (F) (2CG1CR) (M)

(2) MOVES BETWEEN PENS

(a) 3CR 3CR 1CR 3CG 2CR 2CG 1CG 3CG
(F) (M) (+2CG) (F) (+1CG) (+1CR) (+2CR) (M)

(b) 3CR 3CR 2CR+1CR 3CG 2CG+1CG 3CG
(F) (M) (M) (F) (M) (M)

lated because they reflected a common causative agent. If one assumed, for instance, that the movement of an individual vole was entirely random, and took no account of the presence of other voles, a correlation between number of encounters and distance moved, or time active, might well be expected. Such a correlation does indeed exist. Since distance moved and time active are strongly correlated, however, I applied a partial correlation, in which either time active or distance moved is held constant, and was unable to ascribe the correlation of activity and number of encounters to either activity variable alone (Table 12).

A more obvious example of spurious correlations is that observed between distance moved and numbers of moves between pens. Since the distance between the pens is relatively large, a vole which made many moves between pens would obviously move quite a few metres in a 8-hour observation period. Another area where a correlation might be expected if vole movements were random is between the number of encounters and the number of moves between pens; however, no such correlation was found. Thus the number of encounters per vole is independent of number of moves between pens.

While it is instructive to look at the overall activity of individual voles, such figures do not indicate how much time voles actually spend in each others' presence.

Table 12. Correlation and partial correlation coefficients between distance moved (D), time active (T) and number of encounters (E) per vole per trial, according to species involved. Numbers in parentheses indicate level of significance, p , of the correlation coefficient, r ; NS = no significant correlation. Factor in parentheses held constant.

<u>TRIAL</u>	<u>SPECIES</u>	<u>N</u>	<u>D vs T</u>	<u>D vs E</u>	<u>T vs E</u>	<u>D vs E (T)</u>	<u>T vs E (D)</u>
CGCGOG	CG	18	0.927 (<0.01)	0.570 (<0.02)	0.532 (<0.05)	0.242 (NS)	0.012 (NS)
CGCGCR	CG	12	0.769 (<0.01)	0.725 (<0.01)	0.452 (NS)	0.662 (<0.05)	-0.240 (NS)
CGCRCR	CG	6	0.879 (<0.05)	0.605 (NS)	0.771 (NS)	-0.241 (NS)	0.631 (NS)
CGCGCR	CR	6	0.926 (<0.01)	0.699 (NS)	0.475 (NS)	0.781 (NS)	-0.639 (NS)
CGCRCR	CR	12	0.866 (<0.01)	0.790 (<0.01)	0.852 (<0.01)	0.202 (NS)	0.546 (NS)
CRCRCR	CR	18	0.768 (<0.01)	0.388 (NS)	0.461 (NS)	0.060 (NS)	0.276 (NS)

It is possible, for instance, that two voles could be active for the same time period, but by remaining in opposite pens would never meet. In nearly all trials, fortunately, such a situation did not arise; nevertheless, it is important to know the degree of overlap of pairs of voles as it relates to the number of encounters between those individuals. Looking at the first part of this problem, I found a good correlation between the mean of the individual number of minutes active for a pair of voles and the number of minutes they were active together in the same pen. Since the minutes active together and overall activity for the three voles in each trial were not totally independent of each other, Spearman's rank test was used on the data, and produced significant correlations for all four trials (r_s : CgCgCg = 0.88, CgCgCr = 0.73, CgCrCr = 0.77, CrCrCr = 0.88; $df = 16$; $p < 0.01$).

How does this relate to the number of encounters? Once again, because of the interdependence of time active for individual voles within each trial, I have taken the mean value for time active together and numbers of encounters for each trial for species-true triplets. For the interspecific trials, I have taken each inter- and intraspecific component of each trial and taken the mean of that figure, where appropriate, and performed a Pearson correlation test on each group of interacting voles. Of the six possible groups of voles (CgxCg [3Cg], CgxCg [CgCgCr], CgxCr

[CgCgCr], CgxCr [CgCrCr], CrxCr [CgCrCr], CrxCr [CrCrCr]), only two groups showed a significant correlation: CgxCr [CgCrCr] ($r=0.97$, $df=4$, $p<0.002$) and CrxCr [CgCrCr] ($r=0.87$, $df=4$, $p<0.05$). If all 36 pairs of figures from all the trials are pooled, however, a highly significant correlation between minutes active together and number of encounters is obtained ($r=0.87$, $df=34$, $p<0.001$). Thus there is a general overall correlation between these two factors, although it is quite varied from trial to trial.

(e) Quantitative Analysis of Encounters

Having obtained a picture of the trends in activity, I now turn to the results of the specific trials. I found that in spite of the greater number of wins that C. rutilus sustained over C. gapperi in interspecific trials (104 wins to 41 losses for 24 interspecific pairs), most interactions were too inconclusive to be able to state which voles were dominant and which were subordinate. Of 12 interspecific trials, 11 pairs were classifiable, of which eight pairs were C. rutilus dominant over C. gapperi and three pairs were C. gapperi dominant over C. rutilus; and 13 pairs could not be classified. Dominants were defined on the basis of which individuals had significantly more wins than losses over their opponents, as indicated by the chi-squared test (or Fisher's exact test where numbers were small).

The next test I carried out was to see if there was a significant difference in the total number of encounters

between inter- and intraspecific pairs of voles within each trial (Table 13A). I also tested to see if there was a significant difference in the proportions of encounters which comprised mutual avoidance compared to wins/losses (Table 13B). I had postulated that even if the two species do not become segregated by direct aggression, then the number and/or type of interactions between the species would differ from that exhibited within each species. As can be seen from Table 13, however, there is no evidence to suggest that the number of encounters was reduced (or increased) between species, or that the incidence of mutual avoidance was any different inter- or intraspecifically. Indeed, the impression gained from the data is that the majority of voles simply do not exhibit very strong segregational behavior.

Working with the null hypothesis that the proportions would be the same inter- and intraspecifically, I pooled figures from the four trial combinations, and analysed numbers of mutual avoidance relative to wins/losses (Table 14). Statistically significant differences in proportions of these two groups of encounters were found in only three comparisons. The differences shown confirm earlier results that C. gapperi is affected by the presence of C. rutilus, the incidence of mutual avoidance being much lower than that for species-true trials. If the behavioral strategies of the two species were dissimilar, a difference

Table 13. Pairs of male voles engaging in significantly different numbers of encounters (A) and incidence of mutual avoidance (B) compared to wins and losses, according to interspecific and intraspecific encounters. (Data from trials using 2C. gapperi + 1C. rutilus and 1C. gapperi + 2C. rutilus, significance established by Chi-squared test, $p < 0.05$).

(A) <u>NUMBERS OF ENCOUNTERS, E</u>	NUMBERS OF VOLE PAIRS
NUMBERS INTERSPECIFIC E > NUMBERS INTRASPECIFIC E	5
NUMBERS INTERSPECIFIC E < NUMBERS INTRASPECIFIC E	6
NO DIFFERENCE IN NUMBERS INTER- OR INTRASPECIFIC E	12
VOLE PAIRS WITH INSUFFICIENT INTERACTIONS	1
(B) <u>INCIDENCE OF MUTUAL AVOIDANCE COMPARED TO WINS/LOSSES</u>	
MUTUAL AVOIDANCE GREATER IN INTERSPECIFIC E	1
MUTUAL AVOIDANCE LOWER IN INTERSPECIFIC E	0
NO DIFFERENCE BETWEEN MUTUAL AVOIDANCE AND WINS/LOSSES	17
VOLE PAIRS WITH INSUFFICIENT INTERACTIONS	6

Table 14. Differences between proportions of pooled numbers of wins+losses (W/L) to mutual avoidance (MA) for inter- and intraspecific pairs of male voles within each of the four trial triplets, according to Chi-squared test. p levels are given for all significant Chi-squared values; ns = no significant difference between pairs.

TRIPLETS	PAIRS	3CG CGxCG	2CG+1CR CGxCG CGxCR		1CG+2CR CGxCR CRxCR		3CR CRxCR
		80:69	53:20	39:12	34:25	40:15	15:5
3CG	CGxCG	-	$p<0.01$	$p<0.01$	ns	$p<0.05$	ns
2CG+1CR	CGxCG	-	-	ns	ns	ns	ns
	CGxCR	-	-	-	ns	ns	ns
1CG+2CR	CGxCR	-	-	-	-	ns	ns
	CRxCR	-	-	-	-	-	ns
3CR	CRxCR	-	-	-	-	-	-

between the two species-true groups would have been expected, but this was not so, mainly because of the low number of encounters which C. rutilus experienced. A difference is evident between C. gapperi in species-true trials and rutilus/rutilus encounters in the gapperi/rutilus/rutilus trials, however. The only conclusions I can tentatively draw from these data are that C. gapperi appear to exhibit a greater frequency of mutual avoidance in their encounters than C. rutilus, and that when the overall activity of C. gapperi is depressed by the presence of C. rutilus, a greater proportion of encounters is composed of wins/losses. In a sense, then, depression in activity of C. gapperi could be regarded as a form of avoidance behavior in response to C. rutilus and when encounters do occur, fight or flight are the only alternatives.

(f) Index of Aggression

In the preceding section, I analysed encounters simply on the basis of wins, losses and mutual avoidance; I also noted that, compared to the behavioral observations of others, the frequency of overtly aggressive acts was very low, such that dominance could only be ascribed to about one third of the male voles. Since aggression is made up of more components than just fighting, it is useful to consider other, less obvious, aggressive acts and, by using these behavioral characters together, to produce some cumulative

measure, or index, of aggression. Other workers have used various approaches to describe the behavioral components that make up aggression. Healey (1967) used the total of threats and chases to measure aggression in Peromyscus, while Krebs (1970) used attacks per approach in Microtus. Turner and Iverson (1973) used mutual uprights, threats, fights and vocalizations to describe an index of aggression, and also weighted the acts according to frequency of occurrence. Working with C. gapperi, Mihok (1976) recognised seven behavioral characters associated with aggression and defined an index of dominance according to those and other factors.

Scent-marking, although relatively infrequent, appeared to be a characteristic of dominant voles. I found scent-marking more often among dominant and intermediate voles, i.e. those which were dominant to at least one other vole in a triplet, than among subordinate voles (14 out of 22 compared to 2 out of 14), with few of the unclassifiable voles marking (six out of 35). Thus, while the occurrence of scent-marking in Clethrionomys may be associated with dominance, it cannot, on its own, be used as a measure of individual status within a hierarchy.

Of nine characters possibly associated with aggression (stare, approach, attack, chase, flee, avoid, ignore, move to other pen and scent-mark), I found only four that were strongly associated with dominance and aggressiveness.

When tested by a Chi-squared test, the numbers of acts displayed by dominant voles compared to subordinate voles were significantly greater than that expected if the characters were not associated with individual status (Chi-squared values: approach = 40.36, attack = 12.52, chase = 108.98, scent-mark = 15.6; $p < 0.001$ in all cases). The relative frequency of each aggressive act in each vole-pair per trial was then subjected to discriminant function analysis and the mean discriminant function for each of the four factors calculated. I determined the index of aggression for each vole by multiplying the number of occurrences of each aggressive act by its discriminant function and summing the four resultant values. Thus each vole had two indices of aggression, one for each set of interactions with the other two voles in the triplet.

I grouped the indices of aggression for individuals from each species combination in the behavior trials, and found that these values varied significantly ($F = 3.73$, $df = 7, 136$, $p < 0.01$). While there was a trend from maximum aggression in C. gapperi to a minimum in C. rutilus (Table 15), only pairs of C. gapperi in species-true trials were significantly more aggressive than other pairs according to Duncans' multiple range test. However, when aggression indices of the four possible pairs were pooled, I found that not only was C. gapperi considerably more aggressive than C. rutilus in species-true trials but, in interspecific trials, aggressiveness of the former was decreased

Table 15. Mean index of aggression ($\pm$ S.E.) for inter- and intraspecific encounters between C. gapperi and C. rutilus according to the four trial triplets, as derived from discriminant function analysis of aggressive acts. Numbers in parentheses indicate sample size.

TRIAL TRIPLET	VOLE PAIR	MEAN INDEX OF AGGRESSION	
3CG	CG vs CG	5.19 ± 1.19 (36)	} 4.75 ± 0.96 (48)
2CG1CR	"	3.41 ± 1.45 (12)	
"	CG vs CR	1.35 ± 0.42 (12)	} 1.53 ± 0.51 (24)
1CG2CR	"	1.72 ± 0.94 (12)	
2CG1CR	CR vs CG	2.21 ± 1.03 (12)	} 1.95 ± 0.56 (24)
1CG2CR	"	1.68 ± 0.49 (12)	
"	CR vs CR	1.28 ± 0.55 (12)	} 0.69 ± 0.19 (48)
3CR	"	0.50 ± 0.16 (36)	

while that of the latter was increased (Table 15). These figures are similar to those obtained from inter-trial comparisons of levels of activity and numbers of encounters (Tables 7, 9 and 10). Furthermore, the indices of aggression for interspecific encounters indicate that neither species is significantly more aggressive towards the other. Although the difference is not statistically significant, intraspecific aggression appears to be greater than interspecific aggression in C. gapperi in 2CG1CR trials, while in C. rutilus both inter- and intraspecific aggression are approximately equal in 2CG1CR and 1CG2CR trials.

Once again it could be construed that the index of aggression simply reflects the different level of activity of each species; a pooling of data from all trials certainly shows a strong correlation between number of minutes voles spent together and mean index of aggression of the interacting voles ($r = 0.577$, $df = 70$, $p < 0.001$). Since C. gapperi had high scores for aggression and minutes together, and C. rutilus had low scores for the same factors, a strong correlation between the two factors is hardly surprising. When tested in separate trial groups, however, only two of the six trial conditions appear to be correlated (CG x CG: CGCGCG $r = 0.011$, $df = 16$, $p > 0.1$; CGCGCR $r = 0.521$, $df = 4$, $p > 0.1$; CG x CR: CGCGCR $r = 0.699$, $df = 10$, $p < 0.02$; CGCRCR $r = 0.712$, $df = 10$, $p < 0.01$; CR x CR: CGCRCR $r = 0.736$, $df = 4$, $p > 0.05$; CRRCRCR $r = 0.307$ $df = 16$,

$p > 0.1$). Thus I would say that index of aggression is, at best, only weakly correlated with activity and that the differences in aggression in the different trials are not unduly biased by differences in activity. Although Lagerpetz (1969) and Healey (1967) observed that more active animals tended to be more aggressive, Krebs (1970) found no correlation between the two.

Since values of discriminant functions for the four aggressive acts were derived from confirmed dominant and subordinate voles, it would seem reasonable that unclassified pairs of voles which displayed a similar difference in their respective discriminant functions could also be assigned as dominant or subordinate animals. Although there was a considerable overlap of discriminant functions in the dominant group, all subordinate voles were clustered at the low end of the scale and I was able to select a minimum value for dominants and a maximum value for subordinates which segregated 95% of known voles with which to separate the unknowns. Six pairs of C. gapperi and one pair of C. rutilus from species-true trials were assigned, while only two more pairs of voles from interspecific trials were assigned, one with C. gapperi dominant to C. rutilus and one vice versa. Thus no great differences in dominance relations were exposed by taking into account several components of aggresssion instead of merely wins and losses, and 38 of the 72 pairs of voles remain unclassified, which

further supports my contention that neither species has a strong competitive advantage over the other in encounters.

(g) Wounding Data

Several studies have indicated an association between the levels of wounding and aggressive behavior in small mammals, which may in turn be a function of density (Clarke 1956, Rowe et al. 1964, Christian 1971) or season (Lidicker 1973, Turner and Iverson 1973). More recently, Rose and Gaines (1976) have observed that sex, body weight, reproductive condition and season all have an effect on patterns of wounding in two sympatric species of Microtus. Thus it would seem worthwhile to make an examination of the wounding data on the two species of Clethrionomys.

I examined the skins of 78 C. gapperi and 85 C. rutilus, including 80 of the 108 animals used in behavior trials, and tallied the number of bites sustained by each individual. Although subordinate voles appeared to have a greater number of bites than dominants, the difference was not statistically significant (dominants = 9.48 ± 2.92 , subordinates = 16.73 ± 4.32 , $t = 1.44$, $df = 34$, $p > 0.1$). Many of the wounds were obviously old (and so were most likely received prior to capture), but it is not possible to be certain when many of the wounds were inflicted, some probably being sustained during the behavior trials and some afterwards when the voles were placed in breeding pairs. Therefore no correlation between rank and wounding is to be

expected.

The mean number of bites for C. gapperi was 10.23 ± 1.55 ($n = 78$) and for C. rutilus was 6.91 ± 1.56 ($n = 85$), which tends to support the notion that C. rutilus is the less aggressive of the two species; the difference, however, is not statistically significant ($t = 1.51$, $df = 161$, $p > 0.1$). Since females are generally acknowledged to be less aggressive than males (except possibly when pregnant), I then considered the two sexes separately. C. gapperi males had a mean of 11.29 ± 1.98 bites ($n = 48$) and females had 8.53 ± 2.50 bites ($n = 30$); C. rutilus males had 6.52 ± 1.84 bites ($n=48$) and females had 7.41 ± 2.72 bites ($n=27$). Once again, although the trend is apparent for C. gapperi males to have sustained more bites than females, and C. gapperi more bites than C. rutilus, none of the figures are statistically significant according to the t-test (C. g. males versus C. g. females: $t = 0.87$, $df = 76$, $p > 0.1$, C. r. males versus C. r. females: $t = 0.28$, $df = 83$, $p > 0.1$, C. g. males versus C. r. males: $t = 1.76$, $df = 94$, $p > 0.05$, C. g. females versus C. r. females: $t = 0.30$, $df = 65$, $p > 0.1$).

As already mentioned, level of wounding has been correlated with population density, so I have further broken down the data into groups according to whether the voles came from the increase, peak or decline phases of the population (Table 16). Unfortunately, by the time the data are

Table 16. Mean ($\pm$ S.E.) number of wounds sustained by C. gapperi and C. rutilus according to autopsy data on voles from the increase, peak and decline phases of the population. Numbers in parentheses indicate sample size.

		MALES	FEMALES	MALES AND FEMALES
INCREASE	CG	3.8 ± 1.8 (14)	2.7 ± 1.0 (6)	3.5 ± 1.3 (20)
	CR	0.7 ± 0.6 (16)	0.5 ± 1.0 (12)	0.6 ± 0.9 (28)
	CG	19.2 ± 3.5 (18)	14.0 ± 5.5 (12)	17.1 ± 3.0 (30)
PEAK	CR	9.5 ± 4.0 (15)	8.4 ± 6.5 (10)	9.0 ± 3.5 (25)
	CG	8.9 ± 3.2 (16)	6.0 ± 2.5 (12)	7.7 ± 2.1 (28)
	CR	9.4 ± 3.5 (17)	12.3 ± 4.9 (15)	10.8 ± 2.9 (32)

subdivided again to sex, the samples become so small and the amount of within-group variation so large that there is no significant difference between any of the groups, as indicated by Duncan's multiple range test. If the data for males and females are pooled for each species in each population phase, however, some significant differences do become apparent. According to Duncan's multiple range test, C. gapperi from the peak population had significantly more wounds than those from either increase or decline populations, while C. rutilus had significantly fewer wounds in the increase phase than in the other population phases.

The lack of statistical significance in many of these data is aggravated by the fact that each category contains a variable proportion of animals with no bites, thereby reducing the degree of difference in the mean bite numbers as contributed by individuals with differing numbers of bites. Because of this fact, I decided to classify voles into three groups according to the severity of wounding (Figure 9). Inter-group comparisons of the numbers of voles occurring in each wounding class were made by Chi-squared test (Table 17). As can be seen, C. rutilus in all phases of the population tended to have a greater proportion of individuals with no bites than C. gapperi. Wounding severity increased markedly in C. gapperi from the increase to the peak phase and then returned to the pre-peak level in the decline phase. In C. rutilus, wounding increased in a

Figure 9. Numbers of C. gapperi (light stippling) and C. rutilus (heavy stippling) occurring in each wounding class during the increase, peak and decline phases of the population. Wounding classes: 1 = no wounds, 2 = 1-19 wounds, 3 = 20 wounds or more.

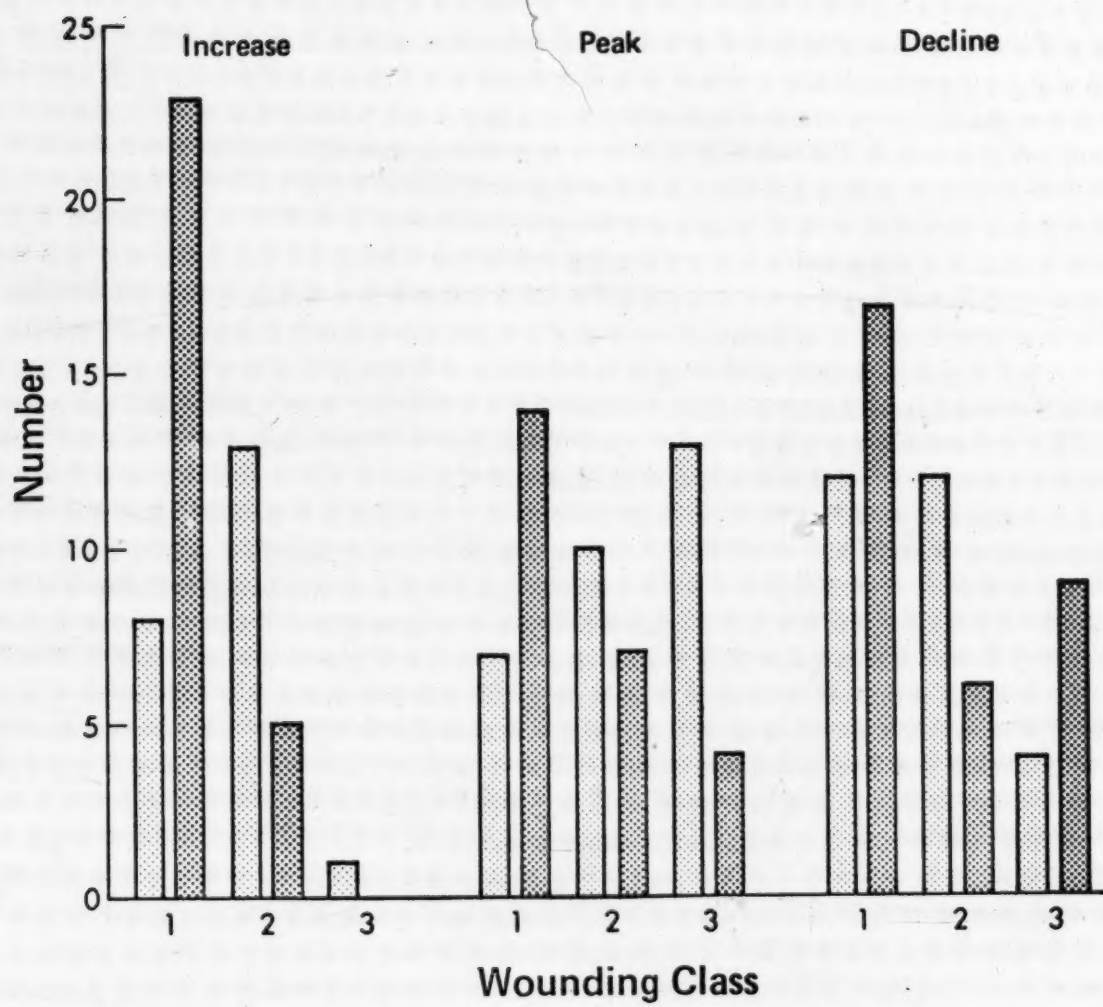


Table 17. Significance values for differences in numbers of voles (as shown in Fig. 9) in each wounding class according to species and phase of population, as indicated by Chi-squared test on 2 x 3 contingency tables. NS indicates no significant difference at 5% probability level.

SPECIES + PHASE	NUMBERS/WOUNDING CLASS			DIFFERENCES BETWEEN SPECIES + PHASE					
	1	2	3	INCREASE	CG PEAK	DECLINE	INCREASE	CR PEAK	DECLINE
CG INCREASE	8	13	1	-	0.01	NS	0.01	-	-
CG PEAK	7	10	13	-	-	0.05	-	0.02	-
CG DECLINE	12	12	4	-	-	-	-	-	NS
CR INCREASE	23	5	0	-	-	-	-	0.02	0.01
CR PEAK	14	7	4	-	-	-	-	-	NS
CR DECLINE	17	6	9	-	-	-	-	-	-

similar fashion, albeit at a much lower level of severity, but did not return to the pre-peak level in the decline phase, such that a significant difference remained between the increase and decline wounding figures.

Thus the observation of a lower incidence of wounding in C. rutilus than C. gapperi appears to be generally confirmed. The higher levels of wounding, both in mean numbers of bites and proportion of severely-wounded animals, during the peak phase than at other phases of the population could be attributed to a preponderance of aggressive individuals in the population (Chitty 1967, Krebs 1970). However, I found no correlation between number of wounds and index of aggression for individual voles ($r = 0.024$, $t = 0.18$, $df = 55$, $p > 0.1$). It is possible that increased wounding was achieved simply by the increased frequency of encounters with other individuals, rather than an increase in aggressiveness per se (Clarke 1955, Archer 1970, Christian 1971). Considering that densities at peak populations in this area are still far below those found further south (Krebs and Myers 1974), I feel that wounding data here probably reflect an increased frequency of encounters rather than an increase in aggressiveness, or proportion of aggressive animals in the population. The lack of correlation between numbers of wounds and genotype (see section on effects of genotype on behavior) tends to support this argument.

(h) Effects of Genotype and Population Phase on Behavior

If aggressive behavior is involved in the regulation of population size in small mammals (Chitty 1967), species that exhibit periodic fluctuations in numbers should show parallel fluctuations in behavior. Chitty (1960) also proposed that a decrease in the fitness of individuals at the peak phase of a population cycle could bring about a decline in that population. A genetic basis to these possible regulatory agents has been hypothesized (Krebs et al. 1973) and although support for this idea has been reported for certain populations (Myers and Krebs 1971, Myers 1974), the connection between genotype and behavior cannot always be made (Krebs 1970, Blackwell and Ramsey 1972, Garten 1976). In laboratory populations, where conditions can be carefully controlled, the effects genotype (Abeelen 1966, Gervais 1976), prior experience (Henderson 1967), maturation (Christian 1971), or a combination of these factors (Lagerspetz 1969) on individual behavior have certainly been demonstrated. Thus it is important to know if such changes were apparent in my trials at the Kakisa River, and whether they affected the outcome of the inter- and intraspecific behavior.

The voles I used in behavior trials came from populations born in 1973, 1974 and 1975, so that individuals from increase, peak and decline phases of the population, as defined by Krebs and Myers (1974), were included. Num-

bers of voles born in each phase were as follows; increase 3 C. rutilus, peak: 22 C. gapperi + 15 C. rutilus, decline; 14 C. gapperi + 18 C. rutilus. Since there were but three voles from the increase phase of the population, I considered individuals from the other two phases only. Animals born into the peak phase appeared to exhibit slightly higher levels of activity in terms of distance moved, minutes active and numbers of encounters per 8-hour activity period, but the difference was not significant according to t-tests applied. Peak and decline phase animals were also found to exhibit no significant differences in index of aggression (C. gapperi: peak = 4.31 ± 1.40 , decline = 2.67 ± 0.94 , $t = 0.86$, $df = 34$, $p > 0.1$; C. rutilus: peak = 1.53 ± 0.49 , decline = 0.90 ± 0.25 , $t = 1.20$, $df = 31$, $p > 0.1$).

It should be noted that a few animals used in behavior trials during the peak year (1974) were overwintered animals born in 1973, and so were increase phase members, whereas young-of-the-year were peak phase members. A number of voles used during the decline year (1975) were overwintered animals born into the peak phase of the population, i.e. during late summer 1974. Since most of the wild voles in the peak population died during the winter of 1974-5, the small portion that survived into the summer of 1975, and which formed the bulk of behavior trial animals in 1975, was presumably a particular remnant of the peak pop-

ulation. In other words, having survived the selection pressures of the post-peak period, these individuals are probably not typical of peak phase animals. If this is so, then the lack of significant differences I observed in activity and aggression between voles from different population phases does not necessarily conflict with the findings of Krebs and others.

Having stated that the effect of population phase is probably not operative in this instance, then, of what consequence is genotype as indicated by homo- and heterozygosity in transferrins, on individual behavior? Since the incidence of transferrin heterozygosity in C. rutilus populations is relatively low (Canham and Cameron 1972), and noting that activity and encounters were too few to observe significant differences within members of this species, I have confined my attention to data on C. gapperi. Unfortunately, I only obtained sera from 29 of the 35 C. gapperi used in behavior trials (16 homozygous, 13 heterozygous), but, in spite of the small sample, I found some interesting results.

First of all, for those individuals for which both serum and hierarchy information was available there are insufficient data to show any dominance advantage of one genotype over the other (dominants: 4 homo + 1 hetero; intermediates: 1 homo + 1 hetero; subordinates: 2 homo + 2 hetero). I then pooled indices of aggression for the two genotypes, and found no difference in levels of aggres-

sion (homo = 4.93 ± 1.88 , hetero = 3.06 ± 0.94 , $t = 0.83$, $df = 27$, $p > 0.1$). However, when I looked at numbers of wins, losses and neutral encounters and levels of activity of the two genotypes, I found that there was a significant difference in proportions of encounters (wins/losses/neutral: homo = 198/148/227, hetero = 86/158/186, Chi-squared = 28.76, $df = 2$, $p < 0.001$), although no significant differences were apparent in mean distance moved and mean minutes active (distance moved: homo = 909 ± 175 , hetero = 714 ± 80 , $t = 0.94$, $df = 27$, $p > 0.1$; minutes active: homo = 163 ± 19 , hetero = 157 ± 12 , $t = 0.25$, $df = 27$, $p > 0.1$). Thus there appears to be a tendency for homozygous voles to win more encounters than heterozygous voles, which is consistent with the hypothesis that homozygotes are the more aggressive type (Myers and Krebs 1971, Krebs et al. 1973, Myers 1974), although other measures of aggression and activity do not support this.

Taking sera data from C. gapperi according to which year they were born in, whether used in behavior trials or not, I found no significant difference in numbers of individuals which were homozygous or heterozygous for transferins (1973: homo = 8, hetero = 7; 1974: homo = 15, hetero = 16; 1975: homo = 8, hetero = 12; Chi-squared = 0.66, $df = 2$, $p > 0.1$). Admittedly, the sample size is small, yet it indicates no trend towards homozygotes in the peak and heterozygotes in the decline phases of the population, as

suggested by others (Canham 1969, Tamarin and Krebs 1969 and 1973, Gaines and Krebs 1971). If I regroup the figures and pool three years' data according to age, there is a suggestion of a difference in proportions among young-of-the-year (overwintered: homo = 22, hetero = 21 young-of-the-year: homo = 9, hetero = 14), although the difference is still not statistically significant (Chi-squared = 0.88, df = 1, $p > 0.1$).

Although I have dealt with the wounding data more fully in another section, I have pooled all the information here on the number of bites sustained for the two genotypes of C. gapperi. As with the activity data, there is no significant difference between the two groups for mean number of bites (homo = 11.2 ± 2.5 , hetero = 11.9 ± 2.7 ; $t = 0.19$, df = 56, $p > 0.1$), or between numbers of voles in the three wounding classes (homo/hetero: 0 wounds = 11/11, moderate wounding = 8/13, severe wounding = 8/8; Chi-squared = 0.78, df = 2, $p > 0.1$). These findings are contrary to what one would expect if one genotype were more aggressive than the other.

From the foregoing considerations, then, I do not feel that population phase has influenced the trials sufficiently to affect the comparison of the behavior of the two species. While there is some suggestion from my data that genic heterozygosity does affect aggressiveness in Clethrionomys, numbers of each genotype were sufficiently dispersed among

the different trial conditions to ensure that very little bias would result. Also, by confining my behavioral observations to the summer months, I was utilizing only reproductively active individuals, so that I avoided the problem of decreased aggression associated with non-reproductive periods of the year (Turner and Iverson 1973).

(i) Radio Telemetry Study

Between 4 January and 11 June 1975, a total of 24 Clethrionomys, comprising 8 male and 5 female C. gapperi and 7 male and 4 female C. rutilus, were introduced into the radio-tracking enclosure. Of these 24 voles, only five were tracked with any degree of success since, even with prior acclimation in the laboratory, many voles died from thermal shock only hours after the commencement of tracking. Other tracking trials failed because of faulty transmitters and, in a few instances, because the vole managed to slip out of the radio collar. Due to a malfunction in the radio receiver system, I was unable to track two voles simultaneously, so I did not obtain any data on the interaction of the two species under an undisturbed snow layer in winter. I was able to collect some information on the activity patterns of the five voles mentioned above, however, and those data are included in the section on circadian and short-term rhythms (q.v.).

During the course of the radio telemetry study I ex-

perienced difficulty in recapturing certain individuals after they had been released into the enclosure. Ten voles were recaptured within 3 days of the traps being set at the perimeter of the enclosure, but two C. rutilus males and one C. gapperi male were not recaptured until 54, 42 and 22 days respectively after being introduced into the enclosure. The 54-day C. rutilus male was recaptured with a female C. gapperi, and the 22-day C. gapperi male was recaptured with a female C. rutilus. Both the females had been introduced (at different times) into the enclosure some while after the males, when I had assumed that the other voles had died. There is evidence that during the winter C. gapperi tend to huddle as a means of increasing the efficiency of thermoregulation (Friesen 1972, Stebbins 1972, Herman 1975), and thus there would be a corresponding decrease in intraspecific aggression. It is interesting to note, therefore, that two species which normally exhibit a high degree of mutual avoidance in summer should be found occupying the same trap in winter.

(j) Circadian and Short-Term Activity Rhythms

Small mammals are known to exhibit circadian rhythms, and the genus Clethrionomys is no exception to this rule. Red-backed voles are generally assumed to be diurnal animals (Brown 1956), yet have been shown to display polyphasic diel activity with peaks of activity around dawn

and dusk (Miller 1955, Buchalczyk 1964, Karulin et al. 1973). The interval between the periods of activity in small mammals can vary from 2 to 5 hours, with the duration of the activity period in C. glareolus reported to range from 0.75 to 2.5 hours (Kikkawa 1964) and 3.5 to 5.9 hours (Karulin et al. 1973). It has also been recognised, however, that circadian rhythms vary according to the season, in response to change in photoperiod (Erkinaro 1961), or latitude (Stebbins 1974), or both (Erkinaro 1972, Stebbins 1972). What information can I derive from my data regarding short-term activity periods and circadian rhythms in Clethrionomys, and to what extent are the behavioral experiments affected by seasonal shifts in circadian rhythms?

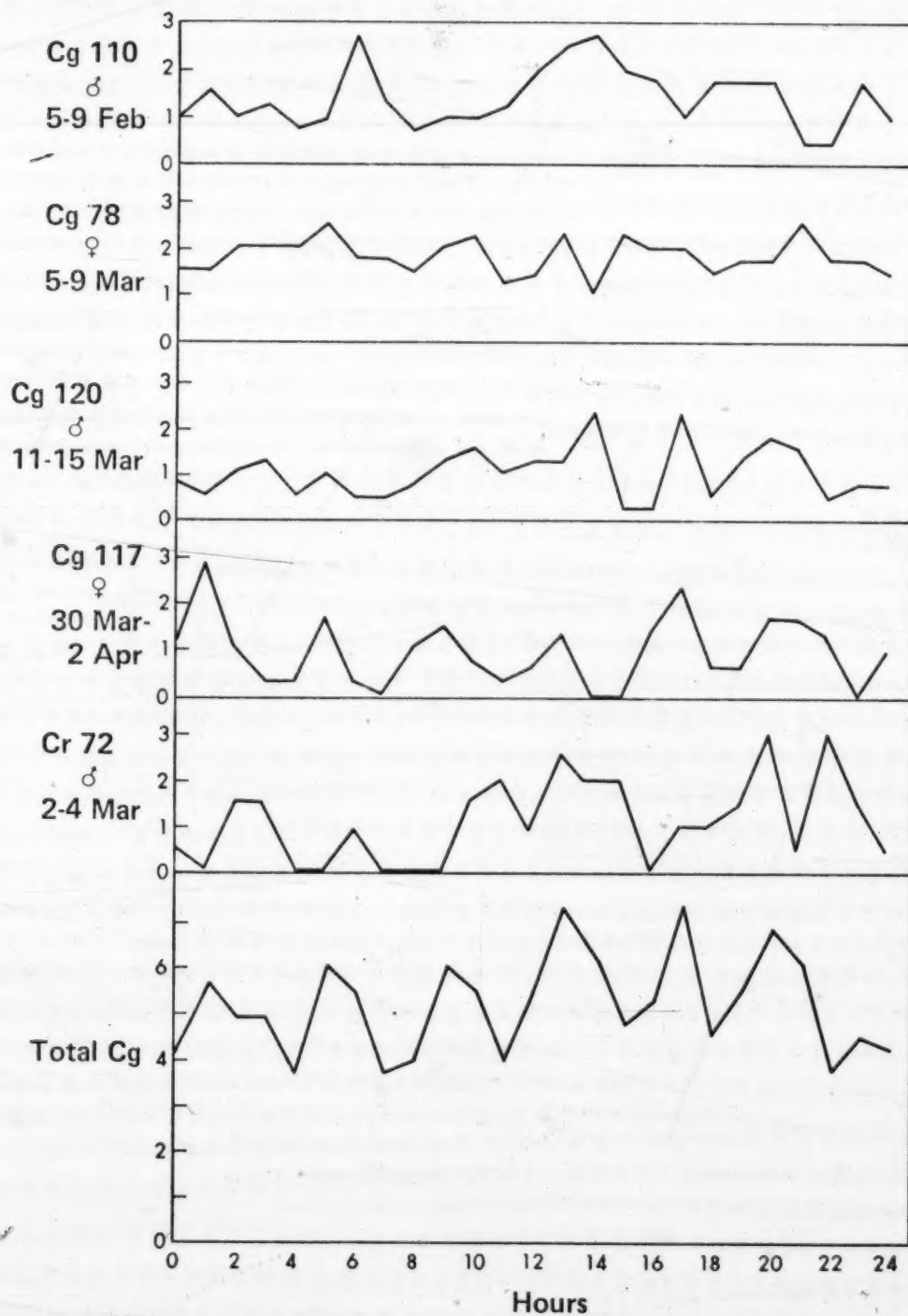
Although I was unable to obtain any information on species interactions during the winter by means of the radio telemetry system at Heart Lake, I did gather some data on the activity of individual voles. The data cover an 8-week period from early February to early April, 1975, during which time the snow depth varied from 48 cm to 64 cm and subnivean temperatures ranged between -9°C and -4°C . In other words, the subnivean environment was relatively stable with little variation in temperature and a sufficient depth of snow to prevent light penetration (Evernden and Fuller 1972). Individual voles were tracked for the lifetime of the transmitter battery, which was generally 4 days, although one battery lasted only 3 days and another lasted

for 2. Activity over a 24-hour cycle was calculated from the mean number of 15 minute periods in each hour in which movement of an individual was noted, averaged over the number of days that it was tracked (Figure 10).

The first thing that is immediately apparent is the polyphasic nature of vole activity, with no strong trend towards diurnal or nocturnal peaks. These data contrast with the findings of Stebbins (1968), who claimed that C. gapperi are nocturnal in winter, and Friesen (1972) and Herman (1975) who maintained that they are diurnal. The discrepancy probably arises from the fact that Stebbins' only winter observations at Heart Lake were during November and December, before sufficient snow had accumulated to bring about light extinction, thus photoperiod could still act as a zeitgeber (Aschoff 1960). During late winter and spring, Herman (1975) showed that C. gapperi tended to revert to nocturnal and crepuscular activity once more, the normal pattern of activity during summer, which Friesen (1972) and Stebbins (1972) also found.

The single activity trace for C. rutilus appears to follow the same polyphasic trend as that in C. gapperi, which agrees with Stebbins (1972), and suggests a basic similarity in activity rhythms of the two species. When the individual activity patterns for C. gapperi are pooled, a strikingly regular pattern of peaks of activity at 4-hour intervals emerges, as has been found in other winter

Figure 10. Individual activity patterns for 4 C. gapperi and 1 C. rutilus based on mean number of 15-minute periods active per hour over the 4 day tracking period, and pooled activity for C. gapperi as revealed by radio-tracking at Heart Lake, winter 1975.



data from Heart Lake (Friesen 1972, Herman 1975).

I conducted all observations on behavior of C. gapperi and C. rutilus between 1st June and 24th August. Since these observations were only composed of two 4-hour periods for the individuals concerned, it is difficult to relate them to circadian rhythms; I have represented the activity rhythms for C. gapperi and C. rutilus over the summer in six time periods of 15-16 days as a mean of the cumulative individual figures, according to minutes active (Figure 11) and distance moved (Figure 12). In calculating these figures, I have not accounted for the proportions of the different combinations of the two species involved in the six time periods, although I recognise that such combinations affect the activity of the individuals concerned. Thus the differences in levels of activity between time periods should not be dwelt upon, except to say that activity appears to be lower in late summer than early summer, possibly as a result of the decline in reproductive activity in the populations.

The most notable feature in both figures is the way in which both species display similar fluctuations of activity in each time period, with C. rutilus continually exhibiting a lower level of activity than C. gapperi. I should point out, of course, that activity during the evening observation period can scarcely be regarded as normal,

Figure 11. Mean number of minutes active per 15 minute period for C. gapperi (solid line) and C. rutilus (dotted line) according to time of year when observations were conducted. Data compiled from activity of males and females. Numbers in parentheses indicate sample size.

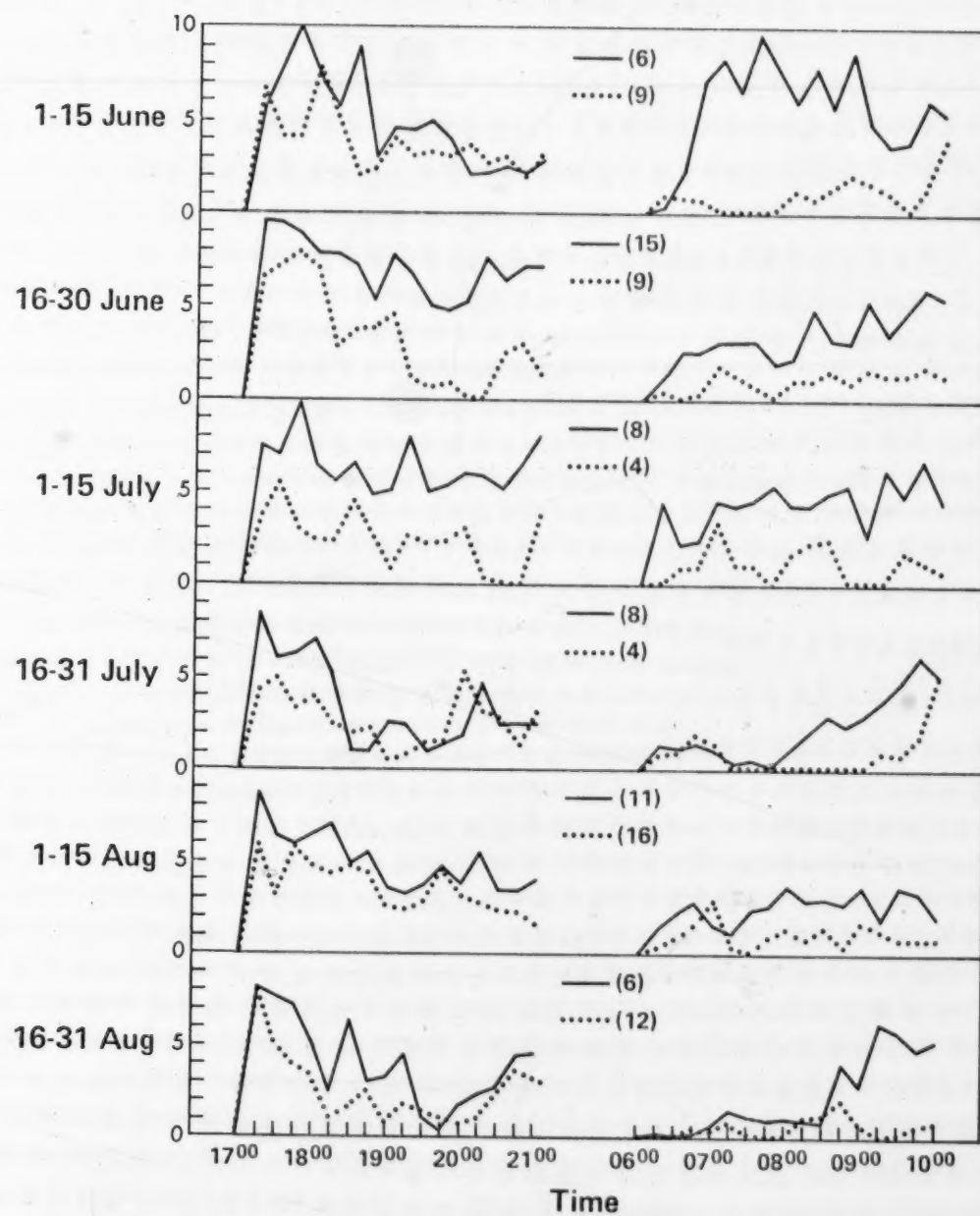
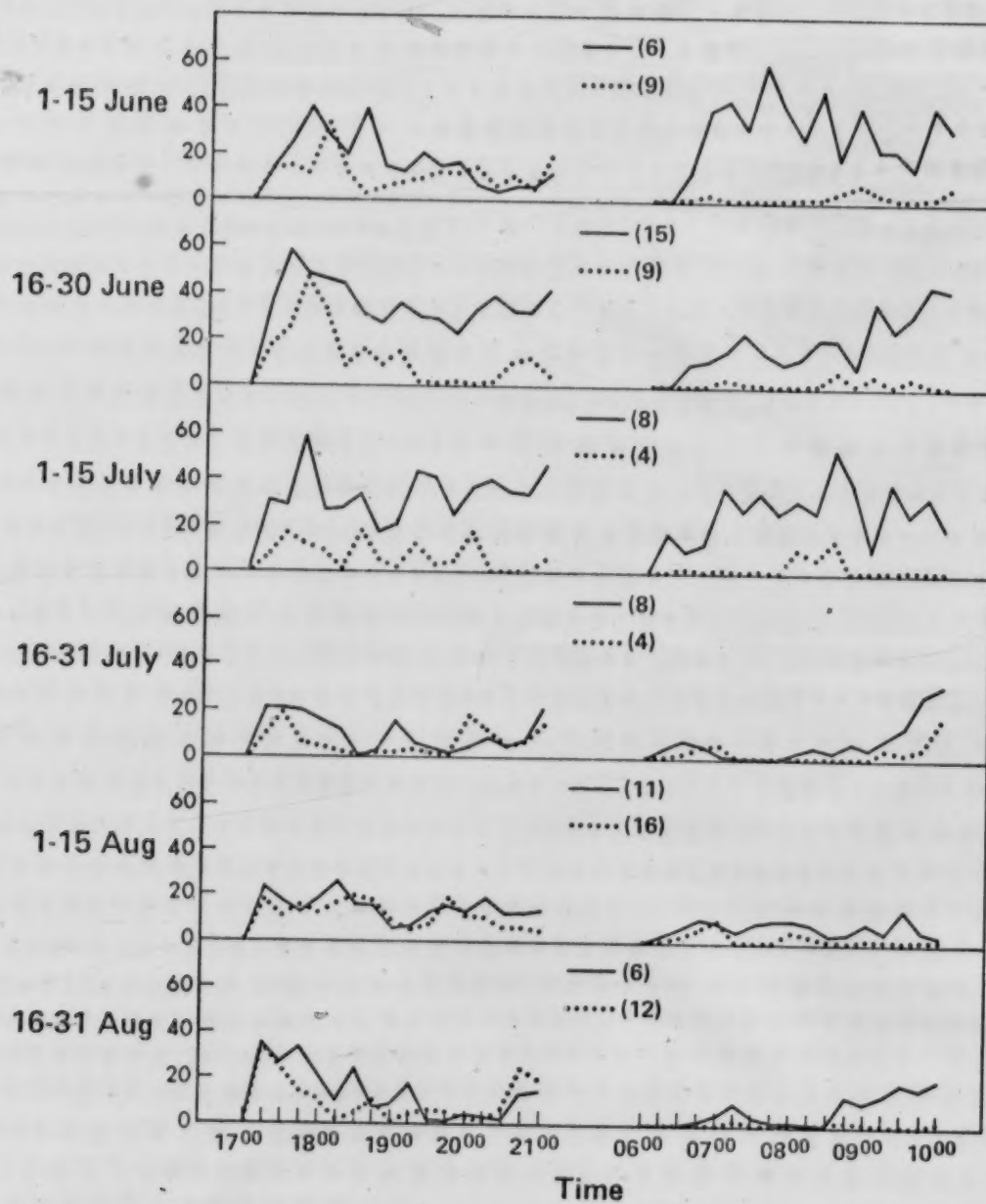


Figure 12. Mean distance moved in metres per 15 minute period for C. gapperi (solid line) and C. rutilus (dotted line) according to time of year when observations were conducted. Data compiled from activity of males and females. Numbers in parentheses indicate sample size.



since voles, freshly introduced into a new environment, were all in an excited state and were spending the first hour or two exploring. After this large peak of activity, most voles settled down to a lower level of activity, one which I presume approximated more closely their normal activity level.

The levels of activity observed the following morning were lower than those of the evening session in all periods, except for C. gapperi in early June. In terms of minutes active, the reduction in activity for all other periods ranged from 65% to 25% of the previous evening's level, and in all periods the reduction in activity was significantly greater (Chi-square, $p < 0.025$) in C. rutilus than it was in C. gapperi. The same reduction was found for the distance moved by C. rutilus, thus lending further support to the hypothesis that C. gapperi is the more "emotional" of the two species and seemed to settle down in confinement less readily than C. rutilus.

It is difficult to detect any definite peaks of short-term activity in any of the graphs. Indeed, it would be surprising if they were detectable, since the 4-hour observation period might at best coincide with two such peaks or, more likely, only a single peak. Other studies have indicated that maximal peaks of summer activity in Clethrionomys occur between dusk and dawn (Miller 1955, Friesen 1972, Stebbins 1972, Herman 1975), although the study by Buch-

alczyk (1964) suggested strong nocturnal activity during August, but no diurnal/nocturnal preference in July or September. At no time did my observations cover the time between sunset and sunrise, direct observations not being possible at such time of course, hence no peaks of maximal activity were seen.

Considering these factors, I feel that the seasonal shift of activity, which is likely occurring during the summer period when my observations were made, was not sufficiently great to prejudice the outcome of the trials using different combinations of voles. Although the onset of light and dark periods is known to be involved in the commencement and cessation of peaks of activity (Erkinaro 1972, Friesen 1972, Herman 1975, Lehmann 1976), the occurrence of smaller bursts of activity and resting appear to alternate more or less regularly, regardless of season. If one ignores such major peaks in Friesen's data, for instance, a more or less regular scatter of minor peaks at any time of the year may be seen, much as the peaks of activity appear to be distributed in my own data (Figures 11 and 12).

One should be extremely careful not to consider short-term and circadian rhythms in complete isolation from each other, however, since there is evidence to show that the latter is indeed based on the former (Stebbins 1975, Lehmann 1976).

DISCUSSION

The concepts of allopatry and sympatry, as they relate to distribution of species, can be readily envisaged. One can easily understand development and perpetuation of distinct species in instances of geographic isolation. Furthermore, when range overlap is observed between two closely related species, closer examination often reveals niche segregation based on allocation of temporal, spatial or resource components. The dynamics of parapatry, on the other hand, are much more difficult to conceptualize. What factors influence the contiguity of two species such that range extension and overlap are seemingly obviated? Inquiries of this nature are often frustrated; sadly, the gaze of the inquirer must be restricted to but a brief moment in time. Any view of species distribution must take into account the temporal component of speciation. This study revolves around the problem of parapatry, illustrated in this instance by two closely related species, Clethrionomys gapperi and C. rutilus. On the basis of my investigations of their present status, and with due regard to aspects of their past history, I have attempted to characterize this parapatric relationship.

One of the first things I was able to discover was

that C. gapperi and C. rutilus are not only capable of crossing the Kakisa River, but have been doing so for at least sixteen years, and probably much longer. Contrary to expectations, there is no evidence to suggest that migration is more frequent in one direction than the other, even though pen studies indicated a much higher level of activity in C. gapperi. My observations of different levels of activity of the two species agree with the findings of Murie and Dickinson (1973), who also suggested that low activity levels in C. rutilus could be an adaptation for reducing energy expenditure which would place them at an increasing competitive advantage to C. gapperi along a latitudinal gradient northward. However, the greater distance covered by C. gapperi in the pens did not appear to be matched by a greater distance moved on the live-trap plot. It could be that this higher level of activity of C. gapperi was merely an artifact of the experimental situation, but if so, why was C. rutilus not affected in a similar way? Even under such conditions of artificiality, then, there appears to be a discernible difference in the behavioral constitution of the two species.

An interesting aspect of behavioral interactions of these species is that the relatively docile C. rutilus was more frequently dominant over the more aggressive C. gapperi in interspecific encounters, and restricted the movement of

the latter. Getz (1962) observed a similar situation in Microtus pennsylvanicus, which was subordinate to the less aggressive M. ochrogaster. It has been suggested that competition between these two species of Microtus has been the main factor limiting the distribution of the two species (Findley 1954). However, Findley indicated that optimal habitat was different for each species, so that each could occupy a variety of habitats in allopatry, but in sympatry the two species were restricted to their optimal habitats, thus reducing direct competition. A similar situation appears to exist between M. pennsylvanicus and M. montanus (Douglass 1976). C. gapperi and Microtus pennsylvanicus have been found to exhibit almost total habitat segregation (Clough 1964, Morris 1969), although of greater interest was the fact that M. pennsylvanicus tended to restrict the movement of C. gapperi in aspen stands more than C. gapperi restricted M. pennsylvanicus in grassland (Morris *ibid*). Restriction of movement of one species by another not only limits the range of habitats which either species might occupy, but also affects their survival when they do occur in sympatry (Caldwell 1964, Sadleir 1965).

Investigations of altitudinal zonation in chipmunks (Eutamias species) have shown that interspecific aggression and habitat preferences serve to reduce species overlap to a minimum (Brown 1971, Sheppard 1971, Heller 1971). Inter-

estingly enough, it has been suggested that aggression has been selected for in two species, E. alpinus and E. amoenus, but not in E. minimus because aggressive interactions in the extreme environment of the hot sagebrush desert in which the latter lives are not feasible for metabolic reasons (Heller 1971, Heller and Gates 1971). It may well be that the low level of aggression observed in C. rutilus could have been selected for during its exposure to a more extreme environment in the past. Unfortunately, there is no study of which I am aware in which the metabolism of these two species of Clethrionomys has been compared, even though the possibility of a physiological difference between C. rutilus and C. gapperi has been suggested (Fuller 1969, Murie and Dickinson 1973). Naturally enough, it is much easier to detect distinct differences over short distances where altitudinal change is concerned than in my own study area, where there is no such zonation of vegetation or climate.

My data do not provide any evidence for preferential traversing of the river during summer or winter, even though it might appear that crossing would be facilitated by a frozen surface. The impetus to migrate is not equal at all times of the year, of course, as it is during periods of high population density and when young voles are dispersing from their natal sites that migration is most

likely (Lidicker 1975, Krebs et al. 1976, Hilborn and Krebs, 1976). A restriction of juvenile access to traps by adult C. gapperi during the summer months was observed by Watts (1970b), which suggested that adults promote juvenile dispersal and migration. Dispersal would tend to be highest during the breeding season (Turner and Iverson 1973), when aggression is highest. Iverson and Turner (1972) also showed that during the fall, a number of C. gapperi migrated into suboptimal grassland habitat normally occupied by Microtus and were able to coexist through winter underneath the snow. Thus migratory tendencies are probably greatest in the summer and fall when the river is still open, and are probably reduced in winter when the river is frozen. Andrzejewski and Wrocławek (1962) observed that resident C. glareolus tended to fill vacant spaces in an area and migrants moved on, while Kozakiewicz (1976) noted such vacant spaces were filled by migrants, which differed qualitatively from residents. It seems likely that invading members of either species would tend to be composed of subordinate, non-breeding, non-territorial individuals, which would be the least fit type for colonising a new area, especially when that area is already occupied by a more numerous species having very similar needs (Narise 1965).

Any indication of the optimal time of year for river crossing could easily be masked by breeding within each

group of voles already established in the range of the other species. Captures of two or three same-aged individuals in the same place and time, suggesting that they may well be littermates born in the range of the other species, may be an indirect sign of breeding. However, no pregnant females of either species have been trapped in the range of the other. While there is little direct evidence of breeding by invading voles, the presence of a number of individuals displaying intermediate specific characters suggests that hybridization is occurring.

A high degree of variation in pelage coloration is known for different species of Clethrionomys. My own observations of museum specimens collected from other parts of the ranges of the two species in northwestern Canada are consistent with these findings. Seasonal variation for any given individual may also be expected. However at the Kakisa River they appeared remarkably distinctive. On the basis of pelage coloration alone, I was able to distinguish over 99% of the specimens captured, while in island and mainland subspecies of C. glareolus, which differ in size, distinction by coat color is not possible (Delaney and Bishop 1960). Identification of a representative sample of C. gapperi and C. rutilus was confirmed by laboratory evaluation of the post-palatal bridge (Hall and Kelson 1959) and the length/width ratio of the nasal foramen. Specimens for which identification by pelage coloration was somewhat dubious were

confirmed in the same manner. Thus it would seem that there is reasonable segregation of the species on pelage characteristics alone. Bolshakov (1963) came to a similar conclusion after analysing the pelage coloration of specimens of C. rutilus and C. glareolus from the Preuralia-Kiznersk region of Udmurt A.S.S.R., where both species were found in the same habitat (Bolshakov 1962), in much the same way as C. gapperi and C. rutilus are found in the Heart Lake area (Fuller 1969, Dyke 1971). In spite of possible overlap in pelage characteristics, then, the species appear to have remained relatively distinct.

From the geographical evidence, is it possible to ascribe a time sequence to the events that led to the separation of C. gapperi and C. rutilus and their subsequent re-expansion to their present distribution? The northern red-backed vole was first recognised as a holarctic species by Coues (1877) and was named Evotomys rutilus. Merriam (1888) regarded the North American form as a distinct species from its Eurasian counterpart and named it Evotomys dawsoni. The name Clethrionomys was given to the erstwhile Evotomys by Palmer (1928), after which five subspecies of the new Clethrionomys dawsoni were recognised by Orr (1945), as well as a new species from St.

Lawrence Island, C. albiventer. Rausch (1950) considered that, on the basis of similarity of skulls and extensive overlap of pelage coloration, C. dawsoni, C. albiventer and the Eurasian C. rutilus warranted inclusion in a single species, C. rutilus, differentiated into subspecies either side of the Bering Straits and on St. Lawrence Island. Manning (1956) reduced the five described North American subspecies of C. rutilus to two, C. r. dawsoni and C. r. washburni, and also described a new subspecies, C. r. platycephalus, from Tuktoyaktuk, Northwest Territories, which bore a closer resemblance to Eurasian subspecies of C. rutilus than to the other North American subspecies. A similar history of naming and renaming has characterised C. gapperi, although the species from the southern Mackenzie area has persisted to the present day as C. g. athabasca, as designated by Preble (1908). It should be remembered, however, that this subspecies is but one representative of a highly polytypic species. The checkered career of the taxonomic status of these species, then, belies their close morphological similarity, which is also born out by their close chromosomal affinities (Rausch and Rausch 1975, Nadler et al. 1976).

Rand (1944) recognised and described C. gapperi and C. rutilus from within 40 miles of each other along the Alaska Highway, and was in no doubt that his specimens

were strictly assignable to one or other of the two species. Recently, Fuller (1969) showed that these species are parapatric at the Kakisa River. Macpherson (1965) also recognised C. gapperi and C. rutilus as distinct species. However, Bee and Hall (1956), on the basis of morphological similarity, considered C. gapperi and C. rutilus to be conspecific, a view most recently upheld by Youngman (1975). More recently, Bee considered that conspecific status for C. gapperi and C. rutilus is less plausible (pers. comm. in Nadler et al. 1976).

With regard to the subspecies of C. rutilus, C. r. platycephalus and C. r. washburni are thought to represent relict populations which have become subspeciated from the main C. rutilus stock during the Wisconsin glacial period in a pair of isolated refugia (Manning 1956). Macpherson (1965) regards both subspecies of C. rutilus as having originated from a common north Beringian ancestor. Bolshakov and Schwartz (1963) noted a striking similarity between Siberian specimens of C. rutilus from the Yamal Peninsula and C. r. washburni, lending further support to the theory of a common ancestor; however, the evidence could also be interpreted as morphological convergence in the subspecies. Manning also suggested an alternative for the origin of C. r. platycephalus, by accidental introduction from Siberia via whaling vessels which called at

Tuktoyaktuk. However, at present there is a general consensus that subspecies of C. rutilus arose during the Wisconsin glacial period. If this is true, then the speciation of C. rutilus and C. gapperi could well be ascribed to an earlier, possibly glacial, period (Holland 1958, Macpherson 1965).

Further clues to the ancestry and past distributions of species of Clethrionomys may be gained from other species which experienced the same glacial history. Rand (1954) views Microtus pennsylvanicus and M. oeconomus as having been similarly separated during the Wisconsin glacial period which, unlike Clethrionomys have established broad overlap in ranges since the breakdown of geographic barriers, although they appear to be ecologically isolated (Cameron 1952). Corbet (1961) commented that Microtus species tend to be far more efficient post-glacial colonizers than Clethrionomys since, as grassland species they would be more adept at invading tundra areas newly-formed by the retreating ice-sheets. This observation is supported by Good (1966), who calculated that M. oeconomus invaded new terrain 30 years after deglaciation, while C. rutilus did not invade until 100 years after. This slower rate of range extension in Clethrionomys during post-glacial times has meant that C. gapperi and C. rutilus have not yet become ecologically isolated. Steven (1955) came to the same conclusion regarding the non-overlap of ranges in C. glareolus and C. rutilus in northern Scandinavia, and

thought that the northward distribution of C. glareolus was, like that of C. gapperi, limited by competition with C. rutilus rather than by environmental factors. C. rufocanus, on the other hand, while overlapping the ranges of both C. glareolus and C. rutilus, is a much larger vole than other Clethrionomys species and appears to occupy quite different habitat from, and thus competes little with, the parapatric pair (Steven ibid).

Both pairs of species of Microtus and Clethrionomys are known to carry distinct species of fleas (Holland 1958). Holland noticed, however, that in their areas of overlap, M. pennsylvanicus were sometimes found to be infested with a flea species normally associated with M. oeconomus. C. rutilus was found to carry a flea Malaraeus penicilliger dissimilis throughout its range in North America (Holland ibid); the same species of flea has been discovered on C. rutilus from Kamchatka (Ioff and Scanlon 1954). In the northern part of its range, C. gapperi is infested with M. p. athabasca, although the differences between this flea and the C. rutilus flea are marked enough for Holland to consider them distinct species. An apparent lack of divergence of the Asian and North American subspecies of C. rutilus is evidenced by their common species of flea; by comparison, much greater difference in the flea complement of the North American species of Clethrionomys is known. The pattern of distribution of their fleas suggests, therefore, that these species of Clethrionomys be-

came speciated before the Wisconsin glacial period. It is interesting to note, however, that less host-specific species of fleas do exist, such as Catallagia dacenkoi, which has been collected from C. rutilus in eastern Asia (as subspecies C. d. ioff), C. gapperi and C. rutilus in North America (as subspecies C. d. fulleri) and even from Microtus species (Holland ibid).

In the light of the ecological aspects of the present-day status of these species, what can be learnt from the paleontological record? Fossil remains of Clethrionomys have been collected from early middle Pleistocene (?Kansan) deposits in China (Kurtén 1968) and northeastern Siberia (Sher 1971), while remains from Illinoian deposits in the latter region have been ascribed to C. rutilus, on the basis of present distribution (Vangengeim 1961). The earliest record of Clethrionomys from North America is of C. gapperi-type remains from deposits of probable Illinoian age in Maryland (Guilday 1971). C. gapperi has also been reported from Wisconsin deposits in Pennsylvania (Hibbard 1958) and other late Pleistocene cave deposits in Tennessee, Illinois and Missouri (Guilday et al. 1969). However, the earliest record of C. rutilus-type remains from North America is that of Harington (1977), who described specimens from late Pleistocene interglacial (?Sangamon) deposits near Old Crow, Yukon Territory. The only other report of Clethrionomys remains from sedimentary

deposits in eastern Beringia is that of Repenning et al. (1964), from the Tofty fauna, Alaska, which is probably of postglacial age.

It should be noted, however, that no method is presently available for separating C. rutilus from C. gapperi and C. glareolus on the basis of skeletal remains alone, so that species assignment has been made purely on the basis of present-day distributions. Even the differing skull features of postpalatal bridge and nasal foramen cannot be used in most species identification, as the only remains that most workers have found have been dentaries (Harington 1977). Thus comments on the dispersal history of red-backed voles are highly speculative.

From the fossil evidence, then, it is apparent that Clethrionomys originated in Europe, probably in late Pliocene time, i.e. more than two million years ago (Harington 1977). If the ancestral form of the genus had an acrocentric male sex chromosome it may first have differentiated into a large C. rufocanus-like form and a smaller form assumed to be C. glareolus-like, in that most early fossils originate from parts of Eurasia that fall within the present-day range of that species. While this form was probably widespread in the temperate forests of Eurasia 500,000 years ago, the northerly C. rutilus-type was not evident until 175,000 years BP, that is, at the beginning of the Illinoian glaciation. This suggests that the latter form diverged from the former, and then spread to North America by 100,000

years BP. Since C. gapperi-type remains are also known from Illinoian deposits in midwestern U.S.A., Clethrionomys had obviously reached North America during or prior to the Illinoian glaciation. Thus it is possible that C. rutilus and C. gapperi diverged from ancestral stock during early Illinoian time, then became separated by the Illinoian glacial period, which lasted from about 175,000 to 100,000 years BP (Hopkins 1967). Contact between these isolates may have been established during the Sangamon interglacial, which lasted from approximately 100,000 to 50,000 years BP, and then again between the Wisconsin glacial maxima around 30,000 years BP, when an ice-free corridor was briefly re-established. It is impossible to say whether or not a significant amount of overlap and genic introgression occurred during these periods of contact, but it seems likely that by the beginning of the Wisconsin glacial, there were already two reasonably well-defined species.

Grant (1974), while acknowledging that his figure was conservative, suggested a period of only 10,000 years for separation of C. gapperi and C. glareolus. But if the closely related subspecies of C. rutilus on St. Lawrence Island and mainland Alaska have been separated for at least 12,000 years, as Rausch and Rausch (1975) claim on the basis of sea-level history in Beringia (Hopkins 1973), a considerably longer period of separation is more likely. Thus, ten-

tative dates for separation between C. gapperi, C. glareolus and C. rutilus range from 30,000 to 200,000 years. Perhaps even these figures are too conservative, since Nadler et al. (1976), in postulating the existence of a trans-Beringian forest-dwelling C. gapperi/glareolus ancestral form, envisaged a holarctic distribution of Clethrionomys about 600,000 years ago, from which C. rutilus was subsequently derived.

How do these estimates of the length of isolation compare with those calculated for other species of Clethrionomys? The situation concerning the British subspecies of C. glareolus is quite fully documented because of the rather complete knowledge of the recent glacial history of Britain and its satellite islands. On this basis, Steven (1953) suggested a period of separation of 7,000 to 9,000 years for offshore island and main island subspecies; Cameron (1965) agreed with this assessment, but Corbet (1961) was of the opinion that subspecies on offshore islands arose from individuals introduced by man as recently as 2,000 years ago from the main island. Corbet considered that the large difference in morphological characters (Steven 1953) and reproductive strategy (Jewell 1966) of subspecies on small islands resulted from the founder effect. Since C. gapperi and C. rutilus are both mainland forms, however, their situation is not totally comparable with the above.

It is also interesting to note that C. g. britannicus from Britain and C. g. glareolus from the European mainland have been distinguished on the basis of a few trivial characters (Hinton 1926) and most likely do not even warrant subspecific status (Corbet 1964), even though they have been separated for as long as the subspecies on off-shore islands have been separated from Britain proper. The production of hybrids from these two forms of C. glareolus in the laboratory (Rauschert 1963), therefore, is not surprising.

A number of attempts have been made to cross-breed other species and subspecies of Clethrionomys. As noted earlier, Steven (1953) and Godfrey (1958) demonstrated that all five British subspecies of C. glareolus were interfertile in the laboratory, and that all the hybrids were also fertile. Spannhof (1960) and Zimmermann (1965) successfully cross-bred C. glareolus X C. rutilus, although the male hybrids were found to be sterile. Sterility was also found with male hybrids of C. glareolus X C. frater produced in captivity (Zimmerman 1965). Zimmermann (*ibid.*) also attempted crossings between C. gapperi X C. glareolus and C. gapperi X C. rutilus, but failed to obtain any progeny. Grant (1974) found that cross-specific breeding was as frequent as species-true breeding between the North American vole, C. gapperi, and the European vole,

C. glareolus. Litter sizes were not significantly different, survivorship of hybrids was no less than that for species-true C. gapperi litters; however, attempts to produce F2 progeny failed. Thus these species, while separated by thousands of miles today, appear to exhibit a lower level of reproductive isolation, than that found between C. gapperi and C. rutilus. My own attempts at cross-breeding between C. gapperi and C. rutilus resulted in but a single litter. All resultant offspring appeared to be abnormally aggressive; Godfrey (1958) observed similar aggressiveness in hybrids of C. glareolus subspecies. Since high levels of aggression affect breeding success (Lagerspetz 1969) and longevity (Christian 1971) in voles, one may infer reduced fitness, and therefore selection against, hybridization in Clethrionomys. However, prolonged exposure of the two populations at the Kakisa River to a certain amount of genetic introgression is no reason for assuming that specific definition is being lost.

While Clethrionomys species have been shown to possess the same diploid number of chromosomes (56), two karyotypic groups have been distinguished by the form of the male sex chromosome (Rausch and Rausch 1975). The form of the male sex chromosome is acrocentric in C. rufocanus, C. occidentalis and C. gapperi, and metacentric in C. glareolus and C. rutilus. Thus the Asian

C. rutilus mikado and North American C. r. dawsoni and C. r. albiventer appeared to have indistinguishable karyotypes, whereas the form of the Y-chromosome differentiated between C. rutilus and C. gapperi in North America.

A more variable number of chromosomes has been noted in different species of Microtus. In the European M. agrestis and North American M. pennsylvanicus, which are thought to have experienced the same length of isolation as C. glareolus and C. gapperi, the same chromosome number of 52 has been found (Matthey 1956), although some differences were noted in the heterosomes. M. oeconomus, on the other hand, was found to have 58-60 chromosomes (Matthey ibid.), which would permit reproductive isolation from M. pennsylvanicus in North America. Isolation is further enhanced, in spite of the considerable overlap of ranges (Youngman 1975), by different habits of the two species (Cameron 1952).

On the basis of data from breeding trials, Grant (1974) considered C. glareolus and C. gapperi to be semispecies, in the terms of Mayr (1963); that is, they exhibit some of the characteristics of separate species and some of the characteristics of subspecies. Some workers consider C. gapperi and C. rutilus to be conspecific (Bee and Hall 1956, Youngman 1975). On the basis of the available evidence for reproductive isolation and the definite evi-

dence for differences in the levels of activity of the two species, I do not believe that such a conclusion is warranted.

Other isolating mechanisms between the two species do not seem, on the face of it, to be well developed. For example, I was able to demonstrate no differences in the general repertoire of behavioral characters between the two species. This is consistent with the findings of Johst (1967) who noted stereotypic patterns of aggressive behavior in several species of Clethrionomys. However, species recognition may involve more subtle nuances of behavior, in which olfactory communication may be important; given the choice, voles tend to select mates from their own kind rather than from another species (Rauschert 1963) or race (Godfrey 1958). A similar situation appears to be prevalent in two closely related species of Peromyscus which, although able to cross-breed in the laboratory, seem to avoid crossing in the wild (Moore 1965). I was certainly able to demonstrate an alteration in levels of activity between interspecific and intraspecific trials, which indicated that species recognition was occurring, and mutual avoidance, a low-intensity form of competitive exclusion, was achieved.

Potential isolating mechanisms may also involve structure and function. Latitudinal variation of these attributes may be expected within and between species. An example of

physiological variation in C. gapperi is evident in differing litter sizes, where southern Alberta populations have fewer young per litter (Skirrow 1969) than northern populations (this study). A similar pattern of latitudinal variation in litter sizes was evident for C. rutilus populations from the Mackenzie Delta (Martell 1975) as compared to populations from the southern boundary of its range (this study). On the other hand, my data indicate no difference in litter size of the two species at the common boundary of their ranges, which suggests convergence under the influence of similar environmental constraints. Variation in external and cranial characters of these species also exhibits clinal patterns (Bee and Hall 1956). A similar clinal change in morphological characters has been observed in subspecies of C. glareolus from France to northern Britain (Corbet 1964). Although proportions of the different transferrins and albumins appeared to remain distinct within each species, biochemical convergence of α -globulins was demonstrated in C. gapperi and C. rutilus (Canham and Cameron 1972).

Thus it appears that morphological and physiological specializations do not noticeably contribute towards isolation of the two species. Morphological convergence does not necessarily require genetic convergence, of course. Morphological convergence accompanied by genetic divergence

has been documented in two species of prairie dogs, Cynomys gunnisoni and C. leucurus (Pizzimenti 1976a, 1976b) whose ranges have come into contact relatively recently. Although hybridization was originally suspected, it was not demonstrated (Pizzimenti ibid.). Genetic divergence has also been demonstrated in pocket gophers (Geomys spp.) presumably as a result of isolation of disjunct populations prior to the Wisconsin glacial period (Penney and Zimmermann 1976), in much the same way as probably occurred in C. gapperi and C. rutilus. Thus there is no reason to assume that the genetic attributes of C. gapperi and C. rutilus are necessarily similar in all respects at their common border simply because they appear to have converged morphologically.

In the preceding pages, I have attempted to outline some aspects of the speciation process in Clethrionomys and, more particularly, to assess the present status of C. gapperi and C. rutilus. Until relatively recently, the study of parapatry and evolutionary processes at species' borders has been largely ignored, or the occurrence of such phenomena merely regarded as anomalous events. Raven (1976), in an excellent review of the present status of systematics at the population level, maintained that the attention of most biologists has all too frequently focused on the study of

discrete units in nature, and the assigning of names to them, in the process of which much useful information on evolutionary, genetic, or ecological principles that govern population dynamics may have been lost. Furthermore, the nature of species is so variable that their use in various kinds of models in population biology may not always be justified.

To be sure, it is a natural tendency for investigators to play safe and seek out predictable situations in well-defined species. The problems of indistinctness at species borders, complexity of gene flow between two supposedly isolated populations and how to detect hybrids in border zones combine to frustrate the researchers' attempts at "pigeon-holing". Yet it is in these very zones where the blurring of specific identity is taking place that research should be directed if the processes involved in speciation are to be elucidated. Thus the situation of parapatry in species, while restricted in time and space compared to the status of single species, is not so much an anomaly but rather a normal adaptive function of populations.

Having acknowledged the inherent difficulty of working in such parapatric situations, then, how do I perceive these species of Clethrionomys as having arrived at their present situation? Considering the five species C. gapperi, C. rutilus, C. glareolus, C. rufocanus and C. occidentalis, there are four general models that could explain their speciation



history. The first model is that all five species diverged at the same point in time from an ancestral type and became progressively isolated; this is unlikely on the basis of present-day geographic distributions and the differing degrees of isolation suggested by their karyotypic patterns.

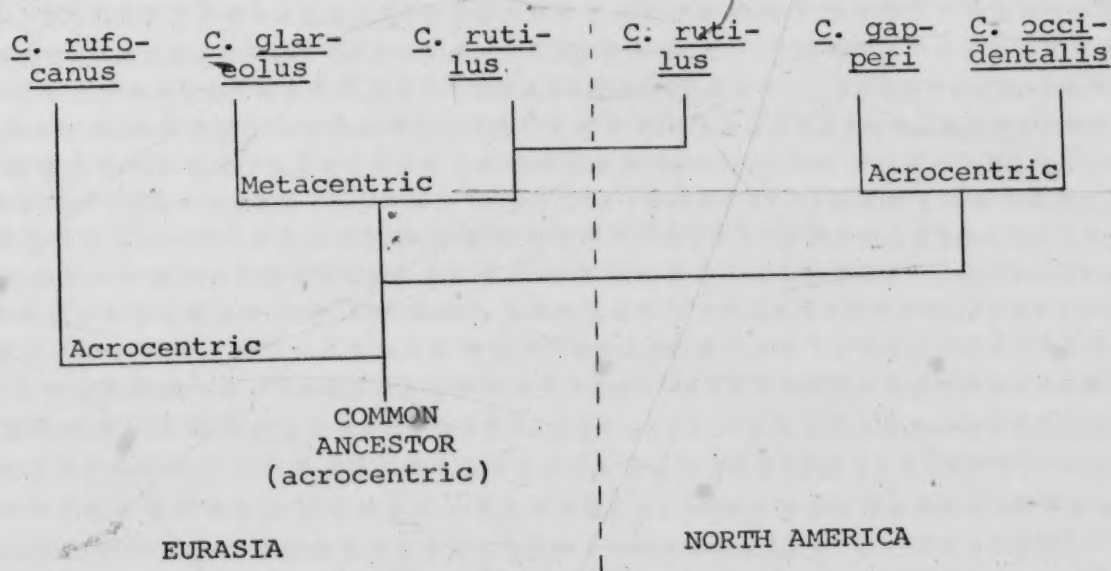
The second model is that C. rutilus diverged from the ancestral form in Eurasia; the ancestral form then spread and invaded North America, became separated from the Eurasian group and the two groups subsequently diverged to form C. gapperi and C. occidentalis in North America, and C. glareolus and C. rufocanus in Eurasia. During a later period, when the Bering land bridge was open once more C. rutilus, which had meanwhile been limited to northern Eurasia, invaded North America and has since established contact with C. gapperi. The relative ease with which crossbreeding has been achieved between C. gapperi and C. glareolus (Grant 1974) supports such a model, but the chromosomal affinities in these species and the need for two major waves of invasion from Eurasia make it less credible.

The third model is that the ancestral form, a C. glareolus-type that arose in Eurasia, diverged into C. glareolus and C. rutilus. The latter spread to North America during the Illinoian, or possibly an earlier glacial period, and became isolated from Eurasian stock which separated into C. glareolus and C. rufocanus. Meanwhile, the C. rutilus-form in North America was separated into three geographically

isolated populations during the next glacial period(s), evolving into C. occidentalis, C. gapperi and C. rutilus, and have since expanded to their present positions. This scheme fits well with present-day distributional patterns, requiring only one major invasion of North America by an earlier form, and ascribing the origin of the genus to a C. glareolus-type, which paleontological evidence tends to support. Also, taxonomists have been more willing to lump C. gapperi and C. rutilus together as conspecifics than C. glareolus and C. rutilus or C. gapperi, which could be taken to indicate their close relations. The scheme does not fit well with the karyotypic data, however, in that C. rufocanus, possessing an acrocentric Y-chromosome, diverged from the metacentric C. glareolus; likewise, the acrocentrically-endowed C. occidentalis and C. gapperi are supposed to have diverged from the metacentric C. rutilus. The occurrence of two identical mutations among these species in two separate continents seems rather unlikely.

The final model, depicted below, is that representatives of the ancestral C. glareolus-type spread to North America where they became geographically isolated and gradually diverged to form C. gapperi. The Eurasian group then developed a metacentric Y-chromosome before diverging to form C. glareolus, a forest-dwelling species, and C. rutilus, a predominantly tundra-dwelling species. Meanwhile, the ranges of the North American form may have been subdivided during a

subsequent advance of the ice, which led to the development of C. gapperi and C. occidentalis as separate species. Finally, C. rutilus may have invaded North America as late as the Wisconsin advance. The chromosomal affinities of C. glareolus and C. rutilus as against C. gapperi and C. occidentalis (Rausch and Rausch 1975) tend to support this model, although it requires two invasions of North America.



Weighing the last two models against each other, there are two negative factors, the need for two separate mutations or the need for two invasions of North America. The two invasions are, in my opinion, the more likely since the Bering land bridge has been formed and severed numerous times, and successive waves of other mammals are known to have invaded North America at different times. Finally, since C. rufocanus is a much larger form than all the other species,

it would seem reasonable that this species would have diverged early on from the ancestral form. Thus the fourth model appears to be the most acceptable, allowing for the present state of knowledge of these species.

In summary, my data indicate that while C. gapperi and C. rutilus may resemble each other and other species morphologically, they are still readily distinguishable at the Kakisa River. They have similar behavior patterns and appear to distinguish between members of their own and other species, and, on the basis of differing levels of activity, exhibit a certain degree of segregational behavior. Reproductive isolation appears to be reasonably well developed, and even though there is evidence of a certain degree of introgressive hybridization, the hybrid zone is probably narrow enough and the rate of gene exchange too low to bring about population fusion. Nevertheless, serum proteins display a clinal variation which could indicate a greater amount of gene exchange. Measurement of the degree of introgression at this common boundary would be a worthwhile further study. A comparative study of the metabolism and physiology of these species would also be of interest, including reproductive aspects such as mate selection, copulatory techniques and fertilization/litter-raising success, in an effort to determine how well (or poorly) segregated they are. Finally, what is happening at other parts of the immense common boundary assumed to exist for these species, from northern

British Columbia to Hudson Bay? Only by taking on the study of such aggravatingly indistinct margins of what have been fondly regarded as discrete species can biologists hope to uncover the processes that govern speciation in nature.

CONCLUSIONS

(1) The Kakisa River forms a mutual boundary for C. gapperi and C. rutilus, yet the river itself does not constitute a barrier to the movement of voles but serves, rather, as a filter.

(2) Individuals of each species were found within the population of the other species, indicating that traversing of the river had occurred, albeit at a relatively low level. There was insufficient evidence to indicate whether the majority of crossings was accomplished during the winter, or at any other time of the year. Since the population on each side of the Kakisa River contained approximately 3% of individuals from the other species, there appears to be no difference in the rate of migration of either species across the river.

(3) Reproductive isolation is reasonably well developed. While copulatory behavior suggested a lack of species discrimination on the part of individual voles, it could be that when presented with a choice, voles would tend to mate with their own kind. Hybridization in these species is possible, albeit at a very low frequency. The highly aggressive nature of the members of the one hybrid litter suggests that hybridization reduced individual fitness and

so would be selected against in natural populations. It is possible that sufficient genetic divergence has occurred to preclude hybridization and population fusion. Only 5%, or less, of these populations appeared to be composed of hybrids.

(4) C. gapperi individuals were considerably more active in the pen situation than C. rutilus in terms of distance moved and length of time active. Evidence for such differences in distance moved in the wild populations on the live-trap plots, however, was inconclusive; hence the results of the pen experiments may reflect a differential response by each species to the experimental situation.

(5) Behavior patterns for both species are noticeably stereotyped, such that no significant differences in qualitative aspects of behavior could be detected between the species. Quantitatively, however, activity of C. gapperi was considerably reduced by the presence of C. rutilus, while the presence of C. gapperi did not appreciably affect activity of C. rutilus. Since C. gapperi is the more aggressive of the two species, reduced activity on its part would result in fewer encounters, hence reduce the frequency of aggressive interactions. While there was a general trend for C. rutilus to be dominant over C. gapperi in trials where dominance was assignable, over half the trials resulted in no dominance. Aggressiveness of C. gapperi towards C. rutilus was also of the same intensity as that

exhibited by C. rutilus towards C. gapperi.

(6) While C. gapperi and C. rutilus exhibit a high degree of morphological and physiological similarity in this region, species integrity has nevertheless been maintained. Ecological requirements of each species are so similar, however, that in sympatry there would be a high degree of competition. Since neither species seems to have a competitive advantage over the other, the expansion of either species into the range of the other is obviated. Thus mutual exclusion appears to be responsible for the maintenance of parapatry in C. gapperi and C. rutilus at the Kakisa River.

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Appendix 1. Details of voles captured during the course of the study and their identification on the basis of pelage coloration (P), condition of the post-palatal bridge (B), and the length/width ratio of the nasal foramen (F). Migration rates for the transferrins relative to the albumins (after Canham and Cameron 1972) are provided for those animals for which serum data are available. All animals were trapped at the Kakisa River, except those marked (**), which were trapped at Fort Providence or Heart Lake. Individuals marked (*) were representatives of one species which were trapped within the range of the other species. A summary of the species identification characters is presented in the final column, where affirmative species characters are indicated by capitals (P, F, B), contrary characters by small letters (p, f, b) and intermediate characters by both (P/p, F/f, B/b).

1974								
SPECIES	NO.	SEX	PELAGE	NASAL FORAMEN	PALATAL BRIDGE	TRANSFERRIN MIGRATION RATES		
						TF1	TF2	
CR	418	F	Red	-	-	-	-	P
CG	420	M	Brown	4.08	Fused	-	54	PFB
CG	421	M	"	4.17	"	-	-	PFB
CG	422	F	"	4.00	"	46	51	PFB
CG	423	F	"	-	-	-	-	P
CG	424	M	"	-	-	-	-	P
CG	425	F	"	-	-	-	-	P
CR	426	M	Red	3.38	Incomplete	46	-	PFB
CR	427	F	"	3.47	"	50	-	PFB
CG	428	F	Brown	-	-	-	-	P
CG	430	F	"	4.08	Fused	-	-	PFB
CG	431	M	"	4.27	"	-	-	PFB
CR*	432	M	Red	3.21	Incomplete	-	-	PFB
CG	433	F	"	3.85	Fused	48	-	pFB
CG	434	F	Brown	3.69	(Damaged)	-	-	PF/f
CG	435	F	Red	3.69	Inc. one side Fused other	-	-	pF/fB/b
CR	436	F	"	3.31	Fused	48	52	Pfb
CG	437	M	Brown	4.08	"	47	-	PFB
CG	438	M	"	3.85	"	47	52	PFB
CG	440	M	"	3.85	"	50	-	PFB
CG	441	M	"	4.17	"	49	54	PFB
CR	442	F	Red	3.50	Incomplete	48	-	PFB
CG	443	F	Brown	3.79	Fused	-	-	PF/fB
CG	444	F	"	3.83	"	-	-	PFB
CR	445	M	Red	3.33	Incomplete	46	-	PFB
CG	446	M	Brown	-	-	-	-	P
CG	447	F	"	4.00	Fused	47	51	PFB
CG	448	M	"	4.42	"	48	52	PFB
CG	450	M	"	3.77	"	-	-	PF/fB
CG	451	M	"	3.92	"	47	53	PFB
CG	452	M	"	4.08	"	-	-	PFB
CG	453	F	"	3.77	"	48	-	PF/fB
CR	454	M	Red	-	-	-	-	P
CR	456	F	"	3.47	Incomplete	-	-	PFB
CR	457	M	"	3.43	"	47	52	PFB
CR	458	M	"	3.47	"	47	-	PFB
CR	460	F	"	3.71	"	47	-	PF/fB
CR	461	F	"	3.67	"	46	-	PF/fB
CR	462	M	"	3.71	"	47	-	PF/fB
CG	463	M	Brown	4.17	Fused	-	-	PFB
CG	464	M	"	-	-	-	-	P
CG	465	M	"	4.25	Fused	-	-	PFB
CG	466	F	"	-	-	49	-	P
CG	467	M	"	-	-	-	-	P

1974 cont.

SPECIES	NO.	SEX	PELAGE	NASAL FORAMEN	PALATAL BRIDGE	TRANSFERRIN MIGRATION RATES		
						TF1	TF2	
CR	468	M	Red	3.40	Incomplete	-	-	PFB
CR	470	F	"	3.31	"	-	-	PFB
CR	471	F	"	3.53	"	-	-	PFB
CR	472	M	"	4.00	"	-	-	PfB
CR	473	F	"	3.71	Fused	46	-	PF/fb
CR	474	M	"	3.47	Incomplete	-	-	PFB
CR	475	M	"	-	-	-	-	P
CR	476	F	"	3.44	Incomplete	46	-	PFB
CG	477	M	Brown	3.69	Fused	-	-	PF/fB
CG	478	F	"	3.75	"	-	-	PF/fB
CG	480	M	"	3.69	"	-	-	PF/fB
CG	481	M	"	3.83	"	-	-	PFB
CG	482	F	"	4.08	"	47	-	PFB
CG	483	F	"	3.70	"	47	53	PF/fB
CG	484	F	"	3.67	"	49	-	PF/fB
CG	485	M	"	3.92	"	-	-	PFB
CR	486	F	Red	-	-	-	-	P
CR	487	F	"	3.57	Incomplete	48	-	PFB
CG	488	M	Brown	-	-	-	-	P
CG	490	F	"	3.71	Fused	-	-	PF/fB
CR	491	M	Red	4.00	Incomplete	-	-	Pf/B
CR	492	M	"	3.07	-	50	-	PF
CR	493	M	"	-	-	-	-	P
CR	494	F	"	3.40	Incomplete	-	-	PFB
CR	495	M	"	-	-	-	-	P
CR	496	M	"	3.67	Fused	-	-	PF/fB
CR	497	M	"	3.47	Incomplete	-	-	PFB
CR	498	M	"	-	-	-	-	P
CR	500	F	"	-	-	-	-	P
CR	501	M	"	3.50	Incomplete	-	-	PFB
CR	502	F	"	-	-	-	-	P
CR	503	F	"	3.47	Incomplete	-	-	PFB
CR	504	M	"	-	-	-	-	P
CR	505	F	"	3.85	Incomplete	-	-	PfB
CR	506	M	"	-	-	-	-	P
CR	507	M	"	3.46	Incomplete	-	-	PFB
CR	508	M	"	3.31	"	-	-	PFB
CG	510	M	Brown	4.00	Fused	-	54	PFB
CG	511	F	"	3.92	"	-	-	PFB
CG	512	-	"	-	-	-	-	P
CG	513	M	"	4.08	Fused	-	-	PFB
CG	514	F	"	-	-	-	-	P
CR*	515	M	Red	3.50	Incomplete	-	-	PFB
CG	516	F	Brown	-	"	-	-	Pb

1974 cont.

SPECIES	NO.	SEX	PELAGE	NASAL FORAMEN	PALATAL BRIDGE	TRANSFERRIN MIGRATION RATES		
						TF1	TF2	
CG	517	F	Brown	3.57	Fused	53	57	Pf/B
CR	518	F	Red	3.69	Incomplete	-	-	PF/fB
CG	520	M	Brown	3.85	Fused	-	-	PFB
CG	521	F	"	3.83	"	-	-	PFB
CG	522	F	"	-	-	-	-	P

1974 C. gapperi 66 x C. rutilus 26 litter

CG/CR	66/26A	M	Red	3.67	Incomplete	48	54	
CG/CR	" B	F	"	3.71	"	49	52	
CG/CR	" C	F	"	3.86	"	49	53	
CG/CR	" D	F	"	4.00	"	49	55	

1974 - Snap-trapped Voles

CR	301	F	Red	3.13	Incomplete	-	-	PFB
CR	302	F	"	-	-	-	-	P
CR	305	F	"	3.36	-	-	-	PF
CR	306	M	"	3.13	Incomplete	-	-	PFB
CR	307	F	"	3.27	"	-	-	PFB
CR	309	M	"	3.27	"	-	-	PFB
CR	310	M	"	3.53	"	-	-	PFB
CR	311	M	"	3.06	-	-	-	PF
CR	312	M	"	3.36	Incomplete	-	-	PFB
CR	313	M	"	3.47	"	-	-	PFB
CR	314	F	"	3.50	"	-	-	PFB
CR	315	M	"	3.47	"	-	-	PFB
CR	317	F	"	3.47	"	-	-	PFB
CR	320	F	"	3.31	"	-	-	PFB
CR	321	M	"	3.13	"	-	-	PFB
CR	322	M	"	3/25	"	-	-	PFB
CG	323	M	Brown	3.77	-	-	-	PF/f
CG	325	M	"	4.08	-	-	-	PF
CG	326	M	"	3.69	Fused	-	-	PF/fB
CR	327	F	Red	3.20	Incomplete	-	-	PFB
CR	328	F	"	3.57	"	-	-	PFB
CR	332	M	"	3.33	"	-	-	PFB
CR	334	F	"	3.53	"	-	-	PFB
CR	335	M	"	3.13	"	-	-	PFB
CG	337	M	Brown	4.83	Fused	-	-	PFB

1975

SPECIES	NO.	SEX	PELAGE	NASAL FORAMEN	PALATAL BRIDGE	TRANSFERRIN MIGRATION RATES		
						TF1	TF2	
CR	1	M	Red	3.93	Incomplete	-	-	PfB
CR	2	M	"	3.40	"	46	-	PfB
CR	3	M	"	3.47	"	-	-	PfB
CR	4	F	"	3.53	"	47	-	PfB
CR	5	M	"	3.79	"	-	-	Pf/fB
CR	6	F	"	3.13	Fused	47	-	PfB
CG	7	M	Brown	4.36	"	-	52	PfB
CG	8	F	"	3.92	"	-	54	PfB
CG	10	M	"	3.92	"	47	51	PfB
CR	11	M	Red	3.79	Incomplete	48	-	Pf/fB
CR*	12	F	"	3.06	"	48	52	PfB
CG	13	F	Brown	4.17	Fused	49	53	PfB
CR	14	M	Red	4.00	-	48	-	Pf
CR	15	M	"	3.40	Incomplete	48	-	PfB
CR	16	M	"	-	-	-	-	P
CR	17	F	"	3.47	Fused	49	-	PfB
CG	18	M	Brown	4.17	"	-	52	PfB
CR	20	M	Red	3.71	Incomplete	48	-	Pf/fB
CR	21	M	"	3.12	"	49	-	PfB
CR	22	M	"	3.53	"	-	-	PfB
CG	23	M	Brown	3.69	Fused	-	-	Pf/fB
CG	24	M	"	4.08	"	48	54	PfB
CG	25	M	"	4.46	"	-	52	PfB
CG	26	M	"	3.69	"	50	54	Pf/fB
CG	27	M	"	4.50	"	49	53	PfB
CG	28	F	"	4.17	"	50	-	PfB
CG	30	F	"	3.85	"	49	52	PfB
CG	31	M	"	-	-	-	-	P
CG	32	M	"	4.17	Fused	51	56	PfB
CG	33	M	"	4.00	"	50	-	PfB
CG	34	M	"	4.00	"	-	-	PfB
CG	35	F	"	3.71	"	-	-	Pf/fB
CG	36	M	"	4.08	"	50	54	PfB
CG	37	F	"	3.69	"	50	-	Pf/fB
CG	38	F	"	4.08	"	50	-	PfB
CR	40	F	Red	3.47	Incomplete	51	-	PfB
CG*	41	F	Brown	4.33	Fused	50	54	PfB
CG	42	M	"	4.37	"	51	-	PfB
CG*	43	M	"	3.85	"	50	54	PfB
CR	44	M	Red	3.53	Incomplete	-	-	PfB
CR	45	M	"	3.64	"	49	-	PfB
CG	46	F	Brown	4.33	Fused	49	-	PfB
CG	47	M	"	4.08	"	-	-	PfB
CR*	48	M	Red	3.47	Incomplete	51	-	PfB

1975 cont.

SPECIES	NO.	SEX	PELAGE	NASAL FORAMEN	PALATAL BRIDGE	TRANSFERRIN MIGRATION RATES		
						TF1	TF2	
CG	50	F	Brown	3.69	Fused	50	54	PF/fB
CG	51	M	"	3.69	"	52	-	PF/fB
CG	52	F	"	3.57	"	-	-	PfB
CG	53	M	"	3.57	"	52	-	PfB
CG	54	F	"	4.00	"	52	56	PfB
CG	55	F	"	3.92	"	51	-	PfB
CG	56	F	"	3.57	"	49	54	PfB
CG	57	M	"	3.92	"	49	-	PfB
CG	58	M	"	3.92	"	56	-	PfB
CG	60	F	"	3.67	"	51	55	PF/fB
CR	61	M	Red	3.50	Incomplete	-	-	PfB
CG	62	F	Brown	3.92	Fused	48	52	PfB
CG	63	F	"	3.73	"	-	-	PF/fB
CR*	64	M	Red	3.62	Incomplete	50	-	PF/fB
CR**	65	F	"	3.50	"	47	-	PfB
CR**	66	F	"	3.31	"	50	-	PfB
CR**	67	M	"	3.47	"	48	-	PfB
CR**	68	F	"	3.67	"	48	-	PF/fB
CR**	70	F	"	3.56	"	48	-	PfB
CR**	71	M	"	3.27	"	47	-	PfB
CR**	72	F	"	3.71	"	47	-	PF/fB
CR**	73	M	"	3.33	"	-	-	PfB
CR**	74	F	"	3.50	"	47	-	PfB
CG	75	M	Brown	3.62	Fused	46	51	PF/fB
CG	76	M	"	3.62	"	48	52	PF/fB
CG	77	F	"	3.54	"	49	53	PfB
CG	78	M	"	3.83	"	49	-	PfB
CG	80	M	"	3.83	"	48	-	PfB
CR**	81	M	Red	3.20	Incomplete	48	-	PfB
CR**	82	F	"	-	-	-	-	P
CR**	83	M	"	3.27	Incomplete	-	-	PfB
CR**	84	F	"	3.64	"	46	-	Pf/fB
CR**	85	M	"	-	-	-	-	P
CR**	86	F	"	3.71	Incomplete	46	-	PF/fB
CR**	87	M	"	3.50	"	47	-	PfB
CR**	88	F	"	3.43	"	48	-	PfB
CR	90	M	"	3.47	Fused	49	-	PfB
CR	91	F	"	3.33	Incomplete	45	-	PfB
CR	92	F	"	3.53	"	48	-	PfB
CR	93	F	"	3.47	"	-	-	PfB
CR	94	F	"	-	-	-	-	P
CR	95	F	"	3.27	Incomplete	47	-	PfB
CR	96	M	"	3.20	"	47	-	PfB
CR	97	M	"	3.57	Fused	46	-	PfB

1975 cont.

SPECIES	NO.	SEX	PELAGE	NASAL FORAMEN	PALATAL BRIDGE	TRANSFERRIN MIGRATION RATES		
						TF1	TF2	
CR	98	M	Red	3.33	Incomplete	-	-	PFB
CR	100	M	"	3.33	"	-	-	PFB
CR	101	F	"	3.86	"	48	-	PFB
CR	102	F	"	3.36	"	48	52	PFB
CR	103	F	"	-	-	-	-	P
CR	104	F	"	-	-	-	-	P
CG	105	M	Brown	3.62	Fused	48	52	PF/FB
CG	106	M	"	4.09	"	47	52	PFB
CR	107	F	Red	3.67	Incomplete	-	-	PF/FB
CR	108	F	"	-	-	-	-	P
CG	110	F	Brown	3.31	Fused	-	-	PFB
CR	111	F	Red	3.31	"	-	-	PFB
CR	112	F	"	3.56	Incomplete	-	-	PFB
CR	113	M	"	3.36	"	-	-	PFB
CR	114	F	"	3.38	"	-	-	PFB
CR	115	M	"	3.57	Fused	48	-	PFB
CG	116	F	Brown	3.77	"	47	-	PF/FB
CR	117	F	Red	3.43	Incomplete	-	-	PFB
CR	118	M	"	3.20	"	-	-	PFB
CG	120	F	Brown	3.75	Fused	49	54	PF/FB
CG	121	M	"	4.08	"	47	51	PFB
CR	122	F	Red	3.25	Incomplete	-	-	PFB
CR	123	M	"	3.50	"	-	-	PFB
CG	124	F	Brown	3.46	Fused	48	52	PFB
CG	125	M	"	4.08	"	52	-	PFB
CR	126	M	Red	3.53	Incomplete	46	-	PFB
CR	127	M	"	2.93	"	-	-	PFB
CG	128	F	Brown	4.00	Fused	47	51	PFB
CG	130	M	"	3.92	"	49	53	PFB
CG	131	M	"	3.83	"	48	-	PFB
CR**	132	M	Red	3.40	Incomplete	48	-	PFB
CR**	133	M	"	3.13	"	47	-	PFB
CR	134	M	"	3.43	"	47	-	PFB
CR**	135	F	"	-	-	-	-	P
CR**	136	F	"	-	-	-	-	P
CR**	137	F	"	-	-	-	-	P
CR**	138	F	"	3.64	Incomplete	46	-	PF/FB
CR**	140	M	"	3.85	"	46	-	PFB
CG**	HL 2	M	Brown	3.50	Fused	48	52	PFB
CG**	HL 3	M	"	4.25	"	48	-	PFB
CG**	HL 5	M	"	4.45	"	-	-	PFB
CG**	HL 6	M	"	4.18	"	-	-	PFB
CG**	HL10	F	"	-	-	-	-	P
CG**	HL11	F	"	3.75	Fused	-	-	PF/FB

1975 cont.

SPECIES	NO.	SEX	PELAGE	NASAL FORAMEN	PALATAL BRIDGE	TRANSFERRIN MIGRATION RATES		
						TF1	TF2	
CG**	HL12	F	Brown	3.50	Fused	-	-	PfB
CG**	HL14	M	"	3.92	"	51	-	PFB
CG**	HL21	F	"	3.62	"	-	-	PF/fB
CG**	HL22	F	"	3.92	"	-	-	PFB
CG**	HL23	M	"	4.00	"	-	-	PFB

Appendix 2

VOLE No.	DISTANCE IN METRES	MINUTES ACTIVE	D/M	ENCOUNTERS			DISCRIM- INANT FUNCTION	INDEX OF AGGRESSION
				WIN	LOSE	NEUTRAL		
440 x 441 x 446	421	87	4.84	1 1	7 11	3 6	1.97 1.97	0.4 0.4
441 x 440 x 446	329	109	3.02	7 8	1 5	3 8	3.51 3.71	6.8 9.1
446 x 440 x 441	560	168	3.33	11 5	1 8	6 8	4.29 3.38	9.9 6.5
18 x 23 x 24	399	116	3.44	2 4	6 0	10 5	2.57 2.76	3.4 2.5
23 x 18 x 24	1185	205	5.78	6 6	2 3	10 12	2.14 2.43	1.3 2.0
24 x 18 x 23	1107	218	5.08	0 3	4 6	5 12	1.83 2.09	0 1.0
HL2 x HL3 x HL14	958	171	5.60	0 3	41 15	9 8	1.97 2.09	0.4 1.0
HL3 x HL2 x HL14	923	174	5.30	41 32	0 2	9 5	6.78 6.61	32.9 25.8
HL14 x HL2 x HL3	1603	212	7.56	15 2	3 32	8 5	3.19 2.16	5.3 1.4
31 x 32 x 33	819	166	4.93	0 0	6 17	11 5	1.97 1.93	0.4 0.3
32 x 31 x 33	546	132	4.14	6 3	0 16	11 9	2.01 2.13	0.6 0.7
33 x 31 x 32	1431	203	7.05	17 16	0 3	5 9	5.19 5.67	15.5 11.9
26 x 27 x 43	1253	210	5.97	5 1	1 9	16 19	3.44 2.68	5.7 2.9
27 x 26 x 43	801	167	4.80	1 0	5 1	16 16	2.41 2.11	1.9 1.1
43 x 26 x 27	1256	188	6.68	9 1	1 0	19 16	4.11 2.87	8.4 3.5
47 x 51 x 53	1370	232	5.91	6 3	6 3	22 22	2.04 2.27	0.7 1.7
51 x 47 x 53	2454	287	8.55	6 15	6 2	22 21	3.08 4.43	5.9 10.5
53 x 47 51	1582	263	6.02	3 2	3 15	22 21	2.52 2.48	2.9 2.3

Distance moved, length of time active, distance/time ratio and analysis of encounters per eight-hour observation period for C. gapperi species-triplets (MALES), including discriminant functions and index of aggression derived from approach, attack, chase and scent-mark data.

VOLE No.	DISTANCE IN METRES	MINUTES ACTIVE	D/M	ENCOUNTERS			DISCRIM- INANT FUNCTION	INDEX OF AGGRESSION
				WIN	LOSE	NEUTRAL		
426 x 445 x 457	361	97	3.72	0	3	0	1.97	0.4
				0	4	0	1.89	0.1
445 x 426 x 457	332	86	3.86	3	0	0	2.36	1.5
				0	8	0	1.93	0.3
457 x 426 x 445	179	51	3.51	4	0	0	2.70	2.6
				8	0	0	3.47	5.2
468 x 474 x 475	214	78	2.74	0	4	2	2.09	1.0
				1	0	1	1.93	0.3
474 x 468 x 475	128	69	1.86	4	0	2	2.06	0.9
				2	0	1	1.97	0.4
475 x 468 x 474	370	98	3.78	0	1	1	1.89	0.1
				0	2	1	2.01	0.6
11 x 14 x 20	186	67	2.78	0	0	0	1.83	0
				1	0	2	1.97	0.4
14 x 11 x 20	97	25	3.88	0	0	0	1.83	0
				0	0	0	1.83	0
20 x 11 x 14	175	72	2.43	0	1	2	1.93	0.3
				0	0	0	1.83	0
71 x 85 x 87	164	76	2.16	0	0	0	1.83	0
				0	1	1	1.93	0.3
85 x 71 x 87	48	50	0.96	0	0	0	1.83	0
				0	1	0	1.83	0
87 x 71 x 85	120	45	2.67	1	0	1	2.00	0.4
				1	0	0	2.00	0.4
126 x 132 x 133	500	126	3.97	0	2	4	1.97	0.4
				0	1	1	1.89	0.1
132 x 126 x 133	333	67	4.97	2	0	4	2.23	1.0
				0	0	1	1.93	0.3
133 x 126 x 132	197	57	3.46	1	0	1	1.93	0.3
				0	0	1	1.83	0
115 x 134 x 140	199	53	3.75	1	0	2	1.89	0.1
				0	0	0	1.83	0
134 x 115 x 140	164	28	5.86	0	1	2	1.93	0.3
				0	1	0	1.83	0
140 x 115 x 134	357	56	6.38	0	0	0	1.89	0.1
				1	0	0	1.89	0.1

Distance moved, length of time active, distance/time ratio and analysis of encounters per eight-hour observation period for C. rutilus species-true triplets (MALES), including discriminant functions and index of aggression derived from approach, attack, chase and scent-mark data.

VOLE No.	DISTANCE IN METRES	MINUTES ACTIVE	D/M	ENCOUNTERS			DISCRIM- INANT FUNCTION	INDEX OF AGGRESSION
				WIN	LOSE	NEUTRAL		
G448 x G450 x R462	1008	153	6.59	18 1	1 11	7 5	5.56 3.26	16.2 4.5
G450 x G448 x R462	609	140	4.35	1 0	18 9	7 1	2.44 1.89	1.7 0.1
R462 x G448 x G450	409	97	4.22	11 9	1 0	5 1	2.73 2.67	2.7 2.7
G451 x G452 x R458	687	173	3.97	8 2	2 7	1 1	3.37 2.63	5.2 2.2
G452 x G461 x R458	299	68	4.40	2 0	8 0	1 1	2.27 1.89	1.2 0.1
R458 x G451 x G452	355	123	2.89	7 0	2 0	1 1	2.67 1.83	2.8 0
G34 x G36 x R44	1457	214	6.81	4 7	11 0	2 5	2.11 2.18	1.1 1.6
G36 x G34 x R44	467	106	4.41	11 5	4 0	2 0	4.73 3.02	10.7 3.4
R44 x G34 x G36	96	52	1.85	0 0	7 5	5 0	1.89 1.83	0.1 0
G57 x G58 x R67	434	136	3.19	4 0	3 6	5 0	2.06 1.97	0.9 0.4
G58 x G57 x R67	285	150	1.90	3 0	4 0	5 0	2.70 1.83	2.2 0
R67 x G57 x G58	123	53	2.32	6 0	0 0	0 0	2.23 1.83	1.0 0
G75 x G80 x R81	583	179	3.26	2 0	0 4	4 2	2.23 1.97	1.2 0.4
G80 x G75 x R81	312	137	2.28	0 0	2 5	4 3	2.00 2.34	0.4 1.3
R81 x G75 x G80	199	84	2.37	4 5	0 0	2 3	1.93 2.71	0.3 2.6
G105 x G110 x R92	597	122	4.89	0 0	0 17	1 4	1.83 2.33	0 1.8
G110 x G105 x R92	37	36	1.03	0 0	0 4	1 1	1.89 1.97	0.1 0.4
R92 x G105 x G110	506	131	3.86	17 4	0 0	4 1	5.09 2.40	12.9 1.4

Distance moved, length of time active, distance/time ratio and analysis of encounters per eight-hour observation period for 2 C. garperi x 1 C. rutilus triplets (MALES), including discriminant functions and index of aggression derived from a proach, attack, chase and scent-mark data.

VERY SMALL PRINTING

VOLE No.	DISTANCE IN METRES	MINUTES ACTIVE	D/M	ENCOUNTERS			DISCRIM- INANT FUNCTION	INDEX OF AGGRESSION
				WIN	LOSE	NEUTRAL		
G7 x R1 x R2	1018	167	6.10	0 0	0 7	0 0	1.89 2.06	0.1 0.9
R1 x G7 x R2	105	48	2.19	0 7	0 0	0 0	2.40 2.84	1.5 3.0
R2 x G7 x R1	119	38	3.13	7 0	0 7	0 0	2.23 1.89	1.0 0.1
G10 x R3 x R5	588	212	2.77	0 1	3 0	5 18	1.97 2.39	0.4 1.7
R3 x G10 x R5	335	77	4.35	3 2	0 2	5 2	2.11 2.23	1.1 1.0
R5 x G10 x R3	392	125	3.14	0 1	1 2	18 2	2.04 1.93	0.7 0.3
G25 x R21 x R22	542	133	4.08	1 3	13 0	2 5	1.93 2.20	0.3 1.1
R21 x G25 x R22	329	124	2.65	13 0	1 6	2 6	2.98 1.83	4.3 0
R22 x G25 x R21	426	120	3.55	0 6	3 0	5 6	1.93 3.47	0.3 6.1
G42 x R45 x R48	1722	272	6.33	2 10	7 6	7 5	2.90 4.85	3.1 11.7
R45 x G42 x R48	381	100	3.81	7 2	2 0	7 3	2.41 1.93	1.9 0.3
R48 x G42 x R45	545	110	4.95	6 0	10 2	5 3	2.41 1.89	1.9 0.1
G76 x R64 x R90	355	94	3.78	1 0	4 1	2 3	1.89 1.89	0.1 0.1
R64 x G76 x R90	150	67	2.24	4 0	1 0	2 0	3.66 1.83	5.8 0
R90 x G76 x R64	204	52	3.92	1 0	0 0	3 0	2.04 1.83	0.7 0
G78 x R96 x R97	125	46	2.72	0 8	0 0	0 3	1.83 2.17	0 1.1
R96 x G78 x R97	256	85	3.01	0 0	0 7	0 4	1.83 2.11	0 1.1
R97 x G78 x R96	490	127	3.86	0 7	8 0	3 4	2.09 2.95	1.0 3.4

Distance moved, length of time active, distance/time ratio and analysis of encounters per eight-hour observation period for 1 *C. gapperi* x 2 *C. rutilus* triplets (MALES), including discriminant functions and index of aggression derived from approach, attack, chase and scent-mark data.

VERY SMALL PRINTING

VOLF No.	DISTANCE IN METRES	MINUTES ACTIVE	D/M	ENCOUNTERS		
				WIN	LOSE	NEUTRAL
434 x 443 x 447	132	41	3.22	1 3	5 0	1 1
443 x 434 x 447	83	50	1.66	5 3	1 2	1 2
447 x 434 x 443	117	41	2.85	0 2	3 3	0 2
482 x 484 x 490	560	182	3.08	1 2	15 5	11 5
484 x 482 x 490	711	203	3.50	15 3	1 5	11 1
490 x 482 x 484	519	120	4.33	5 5	2 3	5 1
HL10 x HL11 x 62	601	145	4.14	1 5	3 0	3 8
HL11 x HL10 x 62	75	32	2.34	3 3	1 1	3 0
62 x HL10 x HL11	283	130	2.18	0 1	5 3	8 0
54 x 55 x 60	139	89	1.56	2 8	0 2	2 9
55 x 54 x 60	115	77	1.49	0 1	2 0	2 4
60 x 54 x 55	388	144	2.69	2 0	8 1	9 4
77 x 116 x 120	233	111	2.10	1 4	0 1	2 6
116 x 77 x 120	243	77	3.16	0 5	1 2	2 4
120 x 77 x 116	557	112	4.97	1 2	4 5	6 4
35 x 124 x 128	102	76	1.34	0 10	0 2	1 4
124 x 35 x 128	248	96	2.58	0 0	0 11	1 1
128 x 35 x 124	730	145	5.03	2 11	10 0	4 1

Distance moved, length of time active, distance/time ratio and analysis of encounters per eight-hour observation period for C. gapperi species-true triplets (FEMALES).

VERY SMALL PRINTING

VOLE No.	DISTANCE IN METRES	MINUTES ACTIVE	D/H	ENCOUNTERS		
				WIN	LOSE	NEUTRAL
418 x 436 x 442	240	55	4.36	0 1	2 7	3 2
436 x 418 x 442	107	41	2.61	2 0	0 1	3 0
442 x 418 x 436	109	40	2.73	7 1	1 0	2 0
461 x 470 x 471	22	13	1.69	0 1	0 0	0 1
470 x 461 x 471	158	37	4.27	0 0	0 0	0 2
471 x 461 x 470	560	126	4.44	0 0	1 0	1 2
65 x 70 x 74	91	31	2.94	0 0	1 2	1 3
70 x 65 x 74	77	48	1.60	1 0	0 0	1 2
74 x 65 x 70	53	48	1.10	2 0	0 0	3 2
72 x 88 x 91	36	18	2.00	0 0	0 0	1 0
88 x 72 x 91	285	77	3.70	0 0	0 0	1 1
91 x 72 x 88	151	61	2.48	0 0	0 0	0 1
40 x 68 x 111	53	31	1.71	0 0	0 0	1 0
68 x 40 x 111	51	39	1.31	0 0	0 0	1 0
111 x 40 x 68	115	41	2.80	0 0	0 0	0 0
4 x 6 x 15	26	19	1.37	0 0	0 2	0 1
6 x 4 x 15	33	26	1.27	0 0	0 0	0 2
15 x 4 x 6	268	52	5.15	2 0	0 0	1 2

Distance moved, length of time active, distance/time ratio and analysis of encounters per eight-hour observation period for C. rutilus species-tru triplets (FEMALES).

VERY SMALL PRINTING